

Mechanistic links between biodiversity effects on ecosystem functioning and stability in a multi-site grassland experiment

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Funding information

National Natural Science Foundation of China, Grant/Award Number: 31988102 and 31870505; National Key Research and Development Program of China, Grant/Award Number: 2017YFC0503906; Deutsche Forschungsgemeinschaft, Grant/Award Number: 319936945/GRK2324; National Science Foundation, Grant/Award Number: DEB-1856318 and CBET-1833988; EU COST Action 852: Quality Legume-Based Forage Systems for Contrasting Environments

Handling Editor: Eric Allan

Abstract

1. Although the positive effects of biodiversity on ecosystem functioning and stability have been extensively documented in the literature, previous studies have mostly explored the mechanisms of functioning and stability independently. It is unclear how biodiversity effects on functioning may covary with those on stability.
2. Here we developed an integrated framework to explore links between mechanisms underlying biodiversity effects on functioning and those on stability. Specifically, biodiversity effects on ecosystem functioning were partitioned into complementarity effects (*CE*) and selection effects (*SE*), and those on stability were partitioned into species asynchrony and species stability. We investigated how *CE* and *SE* were linked to species asynchrony and stability and how their links might be mediated by species evenness, using a multi-site grassland experiment.
3. Our mixed-effects models showed that a higher community productivity was mainly due to *CE* and a higher community stability was mainly due to species asynchrony. Moreover, *CE* was positively related to species asynchrony, thus leading to a positive association between ecosystem productivity and stability.
4. We used a structural equation model to illustrate how species evenness might mediate links between the various mechanisms. Communities with a higher evenness exhibited a higher *CE* and species asynchrony, but a lower *SE* and species stability. These evenness-mediated associations enhanced the positive relationship between *CE* and species asynchrony, but blurred that between *SE* and species asynchrony.
5. *Synthesis*. Our findings demonstrate mechanistic links between biodiversity effects on ecosystem functioning and stability. By doing so, our study contributes a novel framework for understanding ecological mechanisms of the functioning–stability relationship, which has important implications for developing management plans focused on strengthening synergies between ecosystem functioning and stability over the long term.

KEYWORDS

biodiversity effects, complementarity effects, productivity, selection effects, species asynchrony, species evenness, species stability, stability

1 | INTRODUCTION

Decades of experimental studies have provided strong evidence that biodiversity can promote both the functioning and stability of ecosystems (Cardinale et al., 2013; Hooper et al., 2005; Isbell et al., 2015; Tilman et al., 2001, 2006). Two sets of mechanisms have been proposed to account for the positive biodiversity effects on ecosystem functioning (e.g. productivity), namely complementarity effects (*CE*) and selection effects (*SE*) (Loreau & Hector, 2001). *CE* emerge when the average performance of individual organisms is higher in mixtures than in monocultures, due to interspecific differences in resource use or enemy avoidance, or facilitation (Barry et al., 2019; Loreau & Hector, 2001). *SE* emerge when there is a positive covariance between monoculture productivity and relative productivity in mixture, that is, when the mixture is dominated by species with higher monoculture productivity (Loreau & Hector, 2001). Experiments in grasslands and forests have shown that the positive effects of biodiversity on productivity are mainly contributed by *CE* (Cardinale et al., 2007; Huang et al., 2018; Loreau & Hector, 2001; Tilman et al., 2014).

The positive biodiversity effects on ecosystem stability can also be understood from two sets of mechanisms. While stability is a multifaceted concept, temporal stability, as defined by the ratio of temporal mean to standard deviation of ecological properties of interest, has been most widely used in empirical studies (Donohue et al., 2016). Based on the temporal stability measure, recent theory clarifies that community-level stability is determined by two components, that is, species asynchrony and species-level stability (Thibaut & Connolly, 2013; Wang et al., 2019). Thus, species diversity can increase community stability by increasing species asynchrony and/or including species with higher stability (Lehman & Tilman, 2000; Sasaki & Lauenroth, 2011). The former is referred to as the portfolio or insurance effect (Lehman & Tilman, 2000; Yachi & Loreau, 1999). Several experiments in grasslands showed that the stabilizing effects of biodiversity are mainly explained by the portfolio effect, as species stability often decreased, rather than increased with species richness (Hector et al., 2010; Tilman et al., 2006).

Despite these progresses in understanding the mechanisms underlying positive biodiversity effects, previous studies have mostly explored ecosystem functioning and stability independently. That is, very few studies have tested how biodiversity effects on functioning may covary with biodiversity effects on stability (Cardinale et al., 2013; Craven et al., 2018). Using data from 34 biodiversity experiments, Cardinale et al. (2013) conducted a meta-analysis and found that biodiversity effects on ecosystem productivity and stability were both generally positive, but these two effects were largely independent of each other. The lack of a relationship between ecosystem functioning and temporal stability could potentially be explained by idiosyncratic relationships between the different components of biodiversity effects on functioning (i.e. *CE* and *SE*) and stability (i.e. species stability and asynchrony). However, this meta-analysis did not distinguish these mechanisms underlying biodiversity effects and tested their associations.

The mechanisms of ecosystem functioning (*CE* and *SE*) and stability (species stability and asynchrony) can be related in multiple ways, and their relations can be mediated by community structure (Figure 1). A higher *CE*, characterized by interspecific niche complementarity or facilitation, can be associated with lower species asynchrony and higher species stability, due to weak competition and hence reduced compensatory dynamics (Ives et al., 1999; Loreau & De Mazancourt, 2013). However, a higher *CE* may also imply larger differences among species and thus a higher species asynchrony due to species-specific responses to environmental fluctuations (Gonzalez & Loreau, 2009; Wang et al., 2021). A higher *SE*, characterized by the dominance of particular species, can be associated with either higher or lower species asynchrony, depending on whether this dominant species fluctuates more asynchronously or synchronously with other species. Similarly, higher *SE* can be associated with either higher or lower species stability, depending on whether the dominant species have a relatively higher or lower population stability (Wang et al., 2021). Moreover, community structure (e.g. evenness) can mediate the associations between biodiversity effects on functioning and stability. Previous studies have shown that a higher species evenness can increase biodiversity effects on functioning by promoting *CE* (Kirwan et al., 2007) and those on stability through portfolio effects (Isbell et al., 2009b; Wittebolle et al., 2009). Species evenness can also affect *SE* and species stability in either direction, depending on whether more abundant species have higher or lower productivity and population stability. Overall, these potential links between mechanisms of functioning and stability, both direct links and those mediated by species evenness, provide an integrated framework to understand the relationship between functioning and stability (Figure 1).

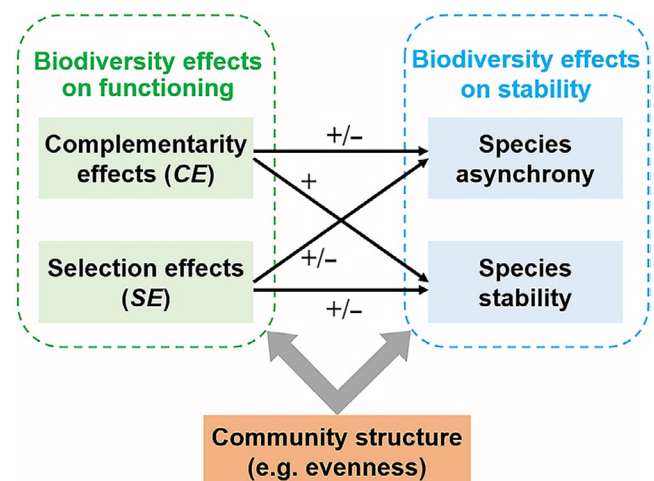


FIGURE 1 A conceptual framework illustrating the potential links between biodiversity effects on ecosystem functioning and stability. Biodiversity effects on functioning (*CE* and *SE*) and those on stability (species asynchrony and species stability) can be related in multiple ways, as illustrated in the main text. Community structure, for example, species evenness, can influence both sets of biodiversity effects and mediates their associations

In this study, we investigated how mechanisms underlying biodiversity effects on functioning and stability were related to each other (Figure 1), using data from a multi-site experiment across Europe and Canada (Kirwan et al., 2014). Using this experiment, previous studies have demonstrated that biodiversity can promote the mean and temporal stability of biomass production, weed suppression and nitrogen yield (Connolly et al., 2018; Finn et al., 2013; Kirwan et al., 2007; Suter et al., 2015). However, it remains unexplored whether biodiversity effects on community productivity and stability are interrelated. As the Agrodiversity experiment manipulated species diversity across a large number of sites using the same protocol and species pool with the same functional composition, it allows us to test the mechanistic links between biodiversity effects on functioning and stability and its generality across sites. Specifically, our analyses aim to answer two questions: (a) Which mechanism (e.g. CE or SE, and species asynchrony or species stability) accounts for biodiversity effects on ecosystem functioning and stability respectively? (b) How are mechanisms of biodiversity effects on functioning (i.e. CE and SE) related to those on stability (i.e. species stability and species asynchrony)?

2 | MATERIALS AND METHODS

2.1 | Data

Our analyses were based on data from 24 sites of the Agrodiversity experiment, a continental-scale coordinated network using the same protocol (Kirwan et al., 2007, 2014). Three years of data were available for each site. At each site, four species were chosen to represent four different functional traits: a fast-establishing grass, a slow-establishing persistent grass, a fast-establishing legume and a slow-establishing persistent legume. Different sites may contain different species, and a total of 9 species were used across all 24 sites (Table S1). Each site contains 30 core plots, representing 15 community types each sown at two seeding densities (i.e. low and high seeding density). The 15 community types include 4 monocultures and 11 four-species mixtures, in which the four species were planted with varying proportions of seeds. Specifically, these 11 mixtures consist of one community where the four species have equal initial proportions of seeds, four communities where one species has an initial proportion of 70% and the other three species each has 10%, and six communities where two species each has 40% and the other two each has 10% (Kirwan et al., 2007). See Kirwan et al. (2014) for details of the experimental design.

The purpose of the design was to quickly establish a strong grass–legume canopy in mixtures to discourage weeds and to maintain the functional benefits of the grass–legume association. Above-ground biomass was measured for each sown species from the first year after sowing. Our analysis of community functioning and temporal stability is based on the above-ground biomass for each sown species for three consecutive years for each core experimental plot

of the selected sites (23 in Europe and 1 in Canada; Table S1). It is worth noting that our analysis does not take into account weeds, which were strongly suppressed in the mixtures but varied greatly between species in monocultures (Connolly et al., 2018). In this experiment, weed is a generic term covering many species, including those sown species that occurred in plots in which they were not initially planted, so the meaning of weeds (e.g. species composition) varies considerably between communities, making it difficult to account for weeds in our framework.

2.2 | Species evenness, ecosystem functioning and stability

We quantified species evenness using the Simpson index: $E = 1 - \sum_{i=1}^S P_i^2$, where P_i is the relative proportion of species i 's seed or biomass in the community. For each mixture community, we defined its initial species evenness (E_{initial}) based on the sown proportion of seeds and the realized species evenness (E_{realized}) based on observed species biomass averaged over 3 years. Previous studies showed that a higher E_{initial} could increase community biomass production in the first year (Finn et al., 2013; Kirwan et al., 2007), but because species composition converges considerably regardless of initial seed proportions, the importance of E_{initial} on community production was much weaker in later years (Brophy et al., 2017). To test the robustness of our results, we also calculated species evenness using the Shannon–Wiener index: $H' = - \sum_{i=1}^S p_i \times \ln p_i$.

We calculated above-ground productivity as the averaged of community biomass over 3 years. The average productivity of species in the monoculture and mixture across 3 years is denoted as M_i and Y_i respectively. The net biodiversity effect (NBE) is defined as the difference between the observed and expected mixture productivity. The expected productivity of species i in the mixture was defined as the product of monoculture biomass and the planted proportion ($RY_{e,i}$). Using the additive partition by Loreau and Hector (2001), we can separate the NBE into CE and SE:

$$NBE = \sum_{i=1}^S (Y_i - RY_{e,i} \cdot M_i) = \sum_{i=1}^S \Delta RY_i \cdot M_i = \underbrace{S \cdot \Delta RY \cdot M}_{CE} + \underbrace{S \cdot COV(\Delta RY, M)}_{SE} \quad (1)$$

Here, $S = 4$ is the number of species, and $\Delta RY_i \triangleq RY_{o,i} - RY_{e,i}$, where $RY_{o,i} = Y_i/M_i$ represents the ratio of species productivity in the mixture to that in the monoculture.

We calculated community stability as the ratio of the temporal mean ($Y_T = \sum_{i=1}^S Y_i$) of community productivity to its standard deviation (σ_T) across 3 years: $S_{\text{com}} = Y_T/\sigma_T$ (Hautier et al., 2014; Tilman et al., 2006). Recent theory showed that community stability could be partitioned into species stability and species asynchrony (Thibaut & Connolly, 2013; Wang et al., 2019). Species stability was defined as the reciprocal of average species variability, which was calculated as: $S_{\text{sp}} = \frac{1}{\sum_i CV_i \times \frac{Y_i}{Y_T}} = \frac{Y_T}{\sum_i \sigma_i}$, where $CV_i = \frac{\sigma_i}{Y_i}$ is the temporal variability of

species i , with Y_i and σ_i denoting the temporal mean and standard deviation of species i . Species asynchrony was defined as the reciprocal of a community-wide metric of species synchrony (Loreau & de Mazancourt, 2008; Wang et al., 2019): $\phi = \frac{\sum_{i=1}^S \sigma_i}{\sigma_T}$. By definition:

$$S_{\text{com}} = S_{\text{sp}} \cdot \phi \quad (2)$$

This partition provides quantitative measures on the two mechanisms that biodiversity stabilizes community productivity, that is, inclusion of more stable species (S_{sp}) and species exhibiting asynchronous dynamics (ϕ).

2.3 | Statistical analysis

We used linear mixed-effects models to examine the overall relationships between community productivity and complementarity effects (CE) or selection effects (SE), as well as the relationships between community stability and species asynchrony (ϕ) or species stability (S_{sp}), with site as the random intercept. Taking the relationship between productivity and CE for illustration, the mixed-effects model is: productivity $\sim CE + (1|\text{site})$. In such models, different sites may be considered as different blocks in the large-scale experiment. We then used similar linear mixed-effects models to investigate the relationships between community productivity and stability, and between biodiversity effects on productivity (CE or SE) and those on stability (S_{sp} or ϕ). In these analyses, both CE and SE were square root transformed to meet assumptions of normality, while retaining their original positive or negative signs (Isbell et al., 2009a). To test the robustness of our results, we re-ran all above analyses using mixed-effects models with both random intercept and slope, for example, productivity $\sim CE + (1 + CE|\text{site})$.

We then used a piecewise structural equation model (SEM; Lefcheck, 2016) to illustrate the relationship between biodiversity effects on functioning and stability. In light of the conceptual framework depicted in Figure 1, we assumed that both CE and SE could affect S_{sp} and ϕ , and that the realized species evenness (E_{realized}) could affect all mechanisms underlying biodiversity effects (i.e. CE , SE , S_{sp} and ϕ). We included the initial species evenness (E_{initial}) as a potential explanatory variable for E_{realized} , although previous studies showed that communities with different initial compositions converge quickly in our study system (Brophy et al., 2017). We also added correlation errors between CE and SE and between S_{sp} and ϕ . Our initial hypothetical SEM is depicted in Figure S1.

All analyses were conducted in R version 4.0.0 (R Core Team, 2020). The linear mixed-effects models were fitted using the `NLME` package (Pinheiro & Bates, 2007). Their goodness-of-fit was measured by marginal and conditional R^2 ($R^2(m)$ and $R^2(c)$ respectively) using the `MuMIn` package, which represents model variation explained by fixed effects and by the combination of fixed and random effects respectively (Nakagawa & Schielzeth, 2013). The SEMs were fitted with local estimation using the `PIECEWISESEM` package (Lefcheck, 2016).

3 | RESULTS

Consistent with previous studies, the mean and temporal stability of total community productivity in mixtures are both higher than those in monocultures, indicating positive effects of biodiversity on both functioning and stability (Figure S2). Higher community productivity in mixtures was mainly driven by higher CE (Figure 2a, $R^2(m) = 0.07$, $R^2(c) = 0.95$, $p < 0.001$), whereas SE contributed weakly to increasing biomass production (Figure 2b, $R^2(m) = 0.0003$, $R^2(c) = 0.94$, $p = 0.291$). Higher community temporal stability was mainly driven by higher species asynchrony (Figure 2c, $R^2(m) = 0.66$, $R^2(c) = 0.93$, $p < 0.001$), although species stability also contributed to stabilizing community productivity (Figure 2d, $R^2(m) = 0.03$, $R^2(c) = 0.77$, $p < 0.001$). These patterns remained unchanged if we used mixed-effects models with both random intercepts and slopes (Figure S3).

We then explored how mechanisms underlying biodiversity effects on productivity were related to those on stability. We found a positive association between CE and species asynchrony (Figure 3a; $R^2(m) = 0.01$, $R^2(c) = 0.71$, $p = 0.013$), but no significant relationship between CE and species stability or between SE and species stability or species asynchrony (Figure S4). Because ecosystem productivity and stability are mainly determined by CE and species asynchrony, respectively (Figure 2), the positive association between CE and species asynchrony eventually translated into a positive association between community productivity and stability (Figure 3b). In other words, communities with a higher community productivity tended to exhibit higher stability. Again, these patterns were robust in mixed-effects models with both random intercepts and slopes (Figure S5).

Our SEM revealed the various links between mechanisms underlying biodiversity effects on ecosystem functioning and stability (Figure 4). Consistent with bivariate results (Figure 3a; Figure S4), species asynchrony was positively related to CE , and species stability was related to neither CE nor SE . But different from bivariate results, species asynchrony also exhibited a positive association with SE . Furthermore, species evenness was associated with all components of biodiversity effects. The initial species evenness (E_{initial}) had a weak positive effect on the realized evenness (E_{realized}). Communities with a higher E_{realized} exhibited a higher CE and species asynchrony, but a lower SE and species stability. All these results were robust when we calculated species evenness using the Shannon–Wiener index (Figures S6).

4 | DISCUSSION

Based on a multi-site experiment, our study shows the intrinsic links between mechanisms underlying ecosystem functioning (CE and SE) and stability (species stability and asynchrony). In particular, we found a positive association between CE , which were the major driver of ecosystem productivity, and species asynchrony, which was the major driver of ecosystem stability. Such a positive association led to a positive relationship between ecosystem productivity

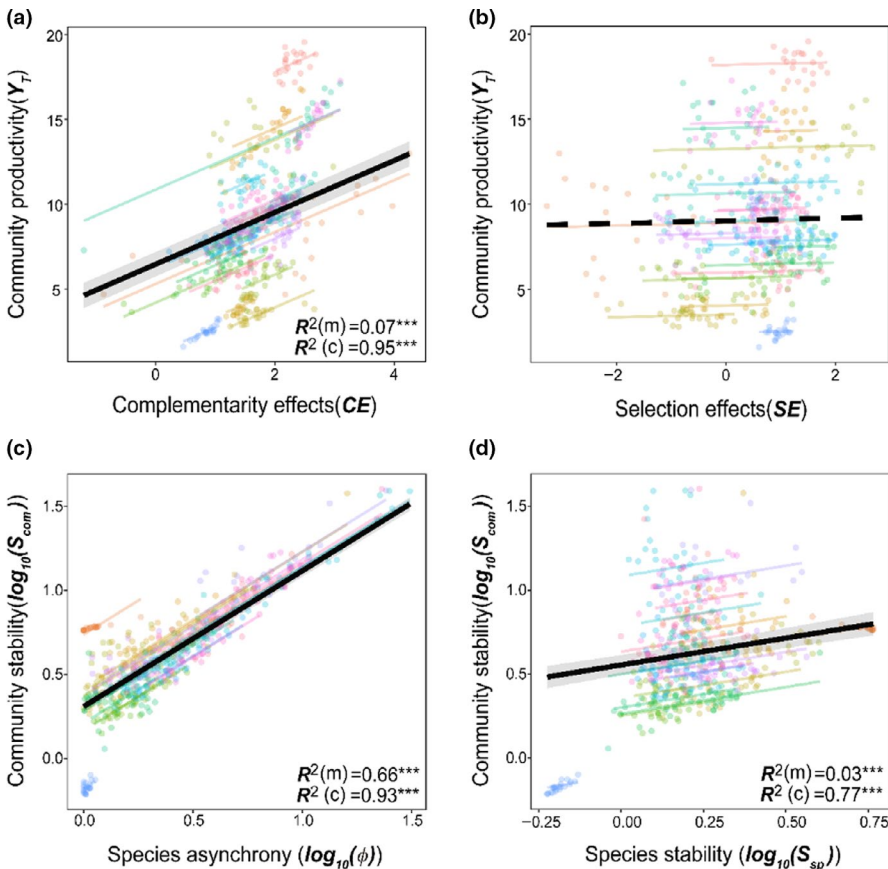


FIGURE 2 Relationships between community productivity and (a) complementarity effects and (b) selection effects, and those between community temporal stability and (c) species asynchrony, (d) species stability. Each point represents one mixture plot, and the different colours represent different sites. CE and SE were square root transformed but retained original positive or negative signs. The solid and dashed black lines indicate significant and insignificant overall relationships, respectively, from the mixed-effects models with site as random intercept, and the coloured lines represent trends within sites. The grey areas indicate the 95% confidence intervals for the regression lines. The $R^2(m)$ and $R^2(c)$ represent model variations explained by fixed effects and the combination of fixed and random effects respectively. Asterisk represents that coefficients are significant: *** $p < 0.001$

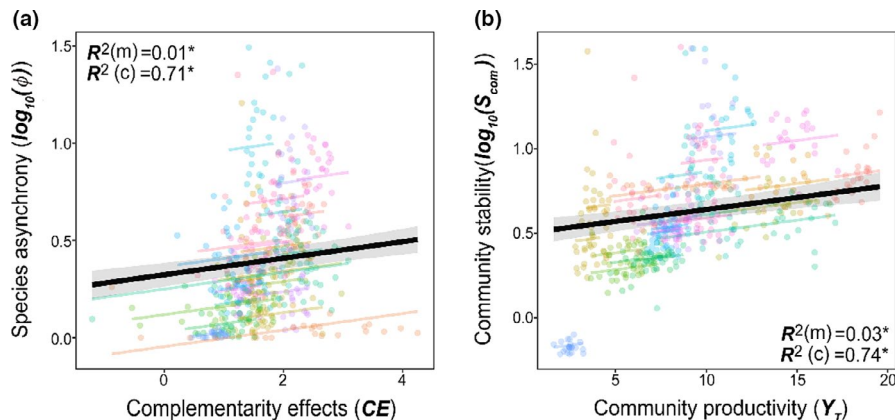


FIGURE 3 Relationships between (a) complementarity effects and species asynchrony and between (b) community productivity and stability. Each point represents one mixture plot, and the different colours represent different sites. CE was square root transformed but retained original positive or negative signs. The black lines represent the fitted relationships from mixed-effects models with site as random intercept, and the coloured lines represent trends within sites. The grey shades indicate the 95% confidence interval for the regression lines. The $R^2(m)$ and $R^2(c)$ represent model variations explained by fixed effects and the combination of fixed and random effects respectively. Asterisk represents that coefficients are significant: * $p < 0.05$

and stability. Our results contribute to an integrated perspective for understanding the mechanisms underlying ecosystem functioning and stability.

Our analyses revealed consistent, positive CE across plots and sites (only five plots with negative CE), which account for the higher ecosystem productivity in mixtures (Figure 2a). In contrast, SE were scattered around zero, although positive values occurred more often (Figure 2b). These results are consistent with findings

from previous grassland and forest experiments (e.g. Cardinale et al., 2011; Fargione et al., 2007; Huang et al., 2018; Loreau & Hector, 2001; Oram et al., 2018). In our study, positive complementarity effects can result from facilitation between grasses and legumes and/or temporal niche complementarity between fast- and slow-establishing species. The presence of legumes can increase the nitrogen pools in the system even with a small proportion, and even after its substantial decline over succession (Finn et al., 2013;

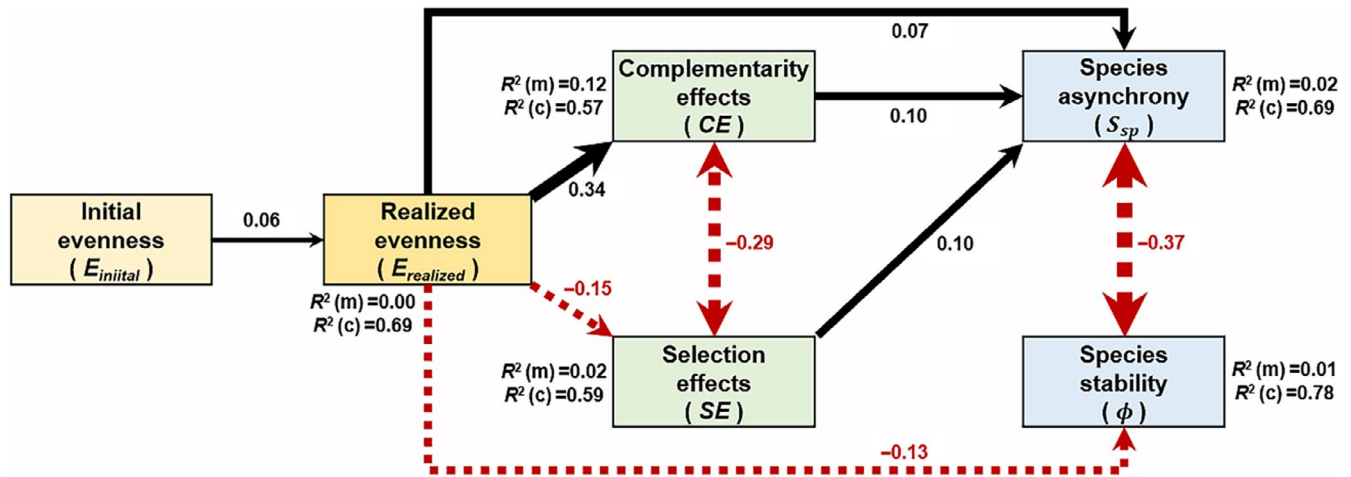


FIGURE 4 Structural equation model (SEM) depicting the relationships between mechanisms underlying biodiversity effects on ecosystem functioning and stability in multi-site. The model was fitted using mixed-effects models with site as the random intercept. Overall the model fit the data well (Fisher's $C = 13.009$, $df = 12$, $p = 0.368$). CE and SE were square root transformed but retain original positive or negative signs. Solid black and dashed red arrows represent significantly ($p < 0.1$) positive and negative pathways respectively. Standardized path coefficients are given next to each (significant) path

Suter et al., 2015). Selection effects occur because our experimental communities are at their early stages of succession and grass species, which have higher monoculture biomass production, become more dominant in the mixture over time (Brophy et al., 2017; Finn et al., 2013). Thus, positive (or negative) SE would emerge, if the community is planted with a low (or very high) initial proportion of grass species. Because succession leads to an increased proportion of grass species and a decreased proportion of legumes, a negative association arises between CE and SE (Figure 4). Such a negative relationship implies that positive CE could be partially offset by negative SE, which corroborates findings from previous experimental studies (Cardinale et al., 2011; Jiang et al., 2008).

Although both species asynchrony and species stability contributed to enhancing ecosystem stability in our experiment, the contribution of species asynchrony was stronger and more consistent across sites (Figure 2). This result is in line with the insurance hypothesis, which states that biodiversity enhances ecosystem stability mainly by promoting species asynchrony (Yachi & Loreau, 1999). In our experiment, species asynchrony could arise from species-specific environmental responses due to their different traits, and/or from the successional process characterized by an increase in some species (e.g. grass species) but a decrease in others (e.g. legumes; Rees et al., 2001). Similarly, a negative association between species asynchrony and species stability emerged (Figure 4), probably because a larger variation in species environmental responses or compensatory dynamics implies a lower species stability, as predicted by competition models (Ives et al., 1999; Loreau & De Mazancourt, 2013).

One key finding from our analyses is that CE and species asynchrony—the major processes driving ecosystem productivity and stability, respectively—were positively related (Figures 3a and 4). Such a positive relationship suggests that processes underlying CE may promote species asynchrony. In our

experiment, temporal niche complementarity between fast- and slow-established species could result in compensatory dynamics in fluctuating environments due to their different rates of population growth (Loreau & de Mazancourt, 2008; Thibaut & Connolly, 2013). Such a perspective from fast-slow economics has increasingly been adopted in recent studies of ecosystem functioning and stability (e.g. Craven et al., 2018; Le Bagousse-Pinguet et al., 2019; Lepš et al., 2018). Moreover, the relationship between complementarity and species asynchrony can also be mediated by species evenness. In our experiment, a higher (realized) species evenness increased both CE, by facilitating interspecific niche complementarity (e.g. fast vs. slow growth) and facilitation (e.g. legume vs. grass; Wittebolle et al., 2009), and species asynchrony, by increasing the effective number of asynchronously fluctuating species (Figure 4; Table S2; Doak et al., 1998; Thibaut & Connolly, 2013). Such a result supports the theoretical prediction of an evenness-mediated synergy between CE and species asynchrony (Wang et al., 2021).

Our SEM also revealed a positive relationship between SE and species asynchrony (Figure 4; Table S2), although it was not supported by bivariate analyses (Figure S4). Such contrasting patterns can be reconciled by the fact that the bivariate relationship combines both direct and evenness-mediated correlation, as revealed by the SEM (Figure 4; Table S2). As explained above, in our experiment SE arose from community succession characterized by an increasing dominance of slow-establishing persistent grass species (Brophy et al., 2017); such compositional shifts resulted in a strong asynchrony between the slow-establishing persistent grass and the other three species (Figure S7). In addition to such a positive, direct association, the increasing dominance by one species implies reduced species evenness, which decreases species asynchrony and creates a negative, indirect association between SE and species asynchrony (Figure 4). This latter result supports the theoretical prediction of an

evenness-mediated trade-off between *SE* and species asynchrony (Wang et al., 2021). Taken together, *SE* are positively associated with species asynchrony, but species evenness mediates a negative association between them (Figure 4; Table S2), which could blur their bivariate relationship.

Because *CE* were positively related with species asynchrony through both direct and evenness-mediated correlation, community productivity and temporal stability exhibited a positive relationship in our experiment (Figure 3). Yet, we should not expect a universal positive productivity–stability relationship, and other relationships can emerge. For instance, if the evenness-mediated negative association between *SE* and species asynchrony balances or even overwhelms the positive association between *CE* and species asynchrony, productivity and stability can be independent or exhibit a trade-off, as predicted by recent theory (Wang et al., 2021). These scenarios may provide possible explanations for the lack of productivity–stability associations from the meta-analysis by Cardinale et al. (2013). We argue that efforts to understand the relationship between functioning and stability should resolve their underlying mechanisms.

While our multi-site dataset allowed us to test the validity of our framework across a large environmental gradient, one shortcoming of this dataset is its relatively short duration (i.e. 3 years) at the early stage of succession, which may induce large uncertainty in estimating stability and species asynchrony. Future empirical work using long-term data is needed to testify the generality of our framework. Moreover, our analyses revealed large across-site variation in the various biodiversity effects underlying ecosystem functioning and stability. In particular, the conditional R^2 is often much larger than the marginal one (Figures 2–4; Figures S3–S6), suggesting that environmental conditions may explain a large proportion of variation for different biodiversity effects. Clarifying how environment may alter biodiversity effects underlying ecosystem functioning and stability and their relationships requires future investigations.

5 | CONCLUSIONS

The past decades of research have greatly advanced our understanding of mechanisms underlying biodiversity effects on ecosystem functioning (i.e. *CE* and *SE*) and stability (i.e. species asynchrony and species stability). How these two sets of mechanisms are interrelated is poorly understood, which, however, has important implications for ecosystem management aimed at achieving high functioning and stability. Our study provides an important step forward by demonstrating mechanistic links between *CE/SE* and species asynchrony, and by showing that such links determine the emergent relationship between functioning and stability. Our theoretical framework (Figure 1) could serve as a benchmark for future studies investigating the relationship between ecosystem functioning and stability. In particular, while our analyses highlighted the role of species evenness, future efforts need to

examine other facets of community structure, such as functional trait composition and phylogenetic relatedness between species (Craven et al., 2018). Such extensions will provide valuable insights for understanding the benefits of ecosystems and guiding management decision making.

ACKNOWLEDGEMENTS

This work was supported by the National Natural Science Foundation of China (31988102, 31870505) and the National Key Research and Development Program of China (2017YFC0503906). J.C. was supported by the International Research Training Group TreeDi funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—319936945/GRK2324. L.J. is supported by the National Science Foundation of USA (DEB-1856318 and CBET-1833988). The Agrodiversity experiment was supported by EU COST Action 852: Quality Legume-Based Forage Systems for Contrasting Environments.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

S.W., Y.Y. and J.C. conceived the idea; Y.Y. analysed the data, with inputs from J.C., M.L., L.J. and S.W.; Y.Y. and S.W. wrote the first draft, and all authors revised the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13725>.

DATA AVAILABILITY STATEMENT

The data used in this paper have been published by Kirwan et al. (2014) (<https://doi.org/10.1890/14-0170.1>). This can be found on Figshare: <https://doi.org/10.6084/m9.figshare.c.3307098.v1> (Kirwan et al., 2016).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Yan, Y., Connolly, J., Liang, M., Jiang, L., & Wang, S. (2021). Mechanistic links between biodiversity effects on ecosystem functioning and stability in a multi-site grassland experiment. *Journal of Ecology*, 109, 3370–3378. <https://doi.org/10.1111/1365-2745.13725>