Title	Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony
Authors(s)	Wang, Shaopeng, Loreau, Michel, de Mazancourt, Claire, Connolly, John, et al.
Publication date	2021-06
Publication information	Wang, Shaopeng, Michel Loreau, Claire de Mazancourt, John Connolly, and et al. “Biotic Homogenization Destabilizes Ecosystem Functioning by Decreasing Spatial Asynchrony.” Wiley, June 2021. https://doi.org/10.1002/ecy.3332.
Publisher	Wiley
Item record/more information	http://hdl.handle.net/10197/25981
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Publisher's version (DOI)	10.1002/ecy.3332

Ecology, 102(6), 2021, e03332

Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony

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Citation: Wang, S., M. Loreau, C. de Mazancourt, F. Isbell, C. Beierkuhnlein, J. Connolly, D. H. Deutschman, J. Doležal, N. Eisenhauer, A. Hector, A. Jentsch, J. Kreyling, V. Lanta, J. Lepš, H. W. Polley, P. B. Reich, J. van Ruijven, B. Schmid, D. Tilman, B. Wilsey, and D. Craven. 2021. Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. Ecology 102(6):e03332. 10.1002/ecy.3332

Abstract. Our planet is facing significant changes of biodiversity across spatial scales. Although the negative effects of local biodiversity (α diversity) loss on ecosystem stability are well documented, the consequences of biodiversity changes at larger spatial scales, in particular biotic homogenization, that is, reduced species turnover across space (β diversity), remain poorly known. Using data from 39 grassland biodiversity experiments, we examine the effects of β diversity on the stability of simulated landscapes while controlling for potentially confounding biotic and abiotic factors. Our results show that higher β diversity generates more asynchronous dynamics among local communities and thereby contributes to the stability of ecosystem productivity at larger spatial scales. We further quantify the relative contributions of α and β diversity to ecosystem stability and find a relatively stronger effect of α diversity, possibly due to the limited spatial scale of our experiments. The stabilizing effects of both α and β diversity lead to a positive diversity–stability relationship at the landscape scale. Our findings demonstrate the destabilizing effect of biotic homogenization and suggest that biodiversity should be conserved at multiple spatial scales to maintain the stability of ecosystem functions and services.

Key words: *β diversity; biotic homogenization; γ diversity; γ stability; grassland experiment; landscape; scale; spatial asynchrony.*

Manuscript received 26 September 2020; revised 6 December 2020; accepted 11 January 2021. Corresponding Editor: Nicholas Gotelli.
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Introduction

Current rates of species extinctions at large scales and simplification of ecosystems at small scales call for a better understanding of the consequences of biodiversity changes across scales (Isbell et al. 2017, Gonzalez et al. 2020). Numerous studies have demonstrated, both experimentally and theoretically, that local diversity (α diversity) loss impairs the functioning and stability of ecosystems (Loreau et al. 2001, Hooper et al. 2005, Tilman et al. 2014). Yet, it remains poorly understood whether findings from these small-scale studies can be extrapolated to predict the consequences of biodiversity changes at larger spatial scales, which are particularly relevant to ecological conservation and management (Gonzalez et al. 2020). One increasingly recognized aspect of biodiversity changes is biotic homogenization, that is, a reduced turnover of species composition across space (reduced β diversity; see Lockwood and McKinney 2001, Dornelas et al. 2014, Magurran et al. 2015, Blowes et al. 2019). Several recent studies started to address the functional consequences of biotic homogenization, showing that the loss of β diversity could decrease multiple ecosystem functions at larger spatial scales (Pasari et al. 2013, Mori et al. 2016, van der Plas et al. 2016, Hautier et al. 2018). Yet the impact of β diversity decline on the stability of ecosystems is not as well understood.

Recent theory predicts that both local biodiversity loss and biotic homogenization (i.e., the loss of α and β diversity, respectively) can reduce the long-term stability of ecosystem functioning at larger spatial scales, but their destabilizing effects are mediated through different pathways (Wang and Loreau 2016). Here, stability is defined as invariability, that is, the ratio of the square mean to the variance (or the inverse of the squared coefficient of variation, $1/CV^2$) of ecosystem productivity (Tilman et al. 2006, Wang and Loreau 2014). Just as regional species diversity (γ diversity or γ_D) can be partitioned into local community diversity (α diversity or α_D) and spatial turnover of species (β diversity or β_D) (Whittaker et al. 1972, Jost 2007), the temporal stability of regional ecosystem productivity (γ stability or γ_S, $1/CV^2$ of total productivity of the regional ecosystem) can be partitioned into two multiplicative components: temporal ecosystem stability at the local scale (α stability or α_S, i.e., $1/CV^2$ of productivity of a local patch) and spatial asynchrony among local communities (ω, i.e., the inverse of the synchrony or temporal coherence of ecosystem productivity among patches; Wang and Loreau 2014). The loss of α diversity is expected to decrease regional γ stability mainly through its negative effect on α stability (Tilman et al. 2006, Hector et al. 2010), although it can also affect spatial asynchrony among local patches (Wang and Loreau 2016). In contrast, the loss of β diversity decreases regional γ stability mainly through its synchronizing effect on ecosystem productivity across local patches. More specifically, a decrease in β diversity increases compositional similarity among patches and thus decreases spatial asynchrony in ecosystem dynamics, because communities with a similar species composition are expected to exhibit more synchronous responses to a common environment than those with different species (Wang and Loreau 2016).

These theoretical predictions offer new insights into how biodiversity impacts ecosystem stability at larger spatial scales. Several recent empirical studies have tested the effects of spatial heterogeneity in biotic and abiotic factors on ecosystem stability at larger scales (McGranahan et al. 2016, Wilcox et al. 2017, Collins et al. 2018, Zhang et al. 2018, Wang et al. 2019). However, these studies were mostly based on observational data (but see McGranahan et al. 2016), in which both diversity and stability responded to different sources of environmental heterogeneity. Spatial variation in environmental conditions or differences in spatial scales may mask the true magnitude and direction of the relationship between biodiversity and stability, because both variables are dependent on the environment and the spatial scale considered (Kraft et al. 2011, Barton et al. 2013, Wang et al. 2017). Thus, a rigorous test of the effect of β diversity (or biotic homogenization) should be performed under the same environmental conditions and spatial scale (e.g., spatial extent, grain size, and sampling intensity). Moreover, recent studies indicate that α and β diversity might interact in regulating ecosystem processes (Wang and Loreau 2016, Hautier et al. 2018). This suggests that the effects of β diversity should be tested, not only under the same abiotic conditions, but also under similar levels of α diversity.

Here, we examine the relationship between β diversity, spatial asynchrony, and the stability of ecosystem productivity using a large data set of 39 grassland biodiversity experiments across North America and Europe. Specifically, we tested the prediction from recent theory that a higher β diversity will increase spatial asynchrony (ω) of ecosystem productivity between local patches, which in turn will enhance ecosystem stability at larger scales (γ stability; Wang and Loreau 2016). Because each experiment manipulated plant species richness under homogeneous environmental conditions at same spatial grains and extents, our data set provides a unique opportunity to test the direct effects of β diversity on ecosystem stability across scales, while controlling for potential confounding effects of biotic and abiotic factors. Because we use data from experiments, however, our approach does not account for spatial processes related to dispersal, which influence β diversity patterns in natural ecosystems (Germain et al. 2017). That said, the theoretical prediction we were testing (i.e., that β diversity increases spatial asynchrony and stabilizes ecosystems at larger spatial scales) was derived under a broad setting of spatial ecological systems, including continuous and discrete landscapes, with and without dispersal (Wang and Loreau 2016, Delsol et al. 2018). In other words, our prediction should hold regardless of the ecological drivers underlying patterns of β diversity (e.g., dispersal, environmental heterogeneity, etc.), although such drivers may influence the effect size of β diversity on spatial asynchrony. We thus examined how the effect of β diversity may be influenced by abiotic and biotic factors. We used a structural equation modeling approach to quantify the relative importance of α and β diversity in stabilizing ecosystem productivity at larger spatial scales, and examined the resulting diversity–stability relationship at the landscape (γ) scale.

Materials and Methods

Experimental data

Our analyses were based on a data set consisting of 39 grassland biodiversity experiments across North America and Europe (Appendix S1: Table S1), which was compiled by Isbell et al. (2015) and Craven et al. (2018). The 39 experiments were originally designed to study the relationships between species diversity and ecosystem functioning and stability at local spatial scales, and manipulated species richness and measured aboveground plant productivity for at least 3 yr. Although most experiments collected data for 3 yr, five collected data for at least 10 yr (Appendix S1: Table S1). Four levels of planted species richness, that is, $\alpha_{\text{planted}} = 1$, 2, 4, and 8, were most commonly used, each occurring in >10 experiments. All other levels of α_{planted} occurred in less than five experiments. Detailed descriptions of these experiments can be found in Isbell et al. (2015) and Craven et al. (2018).

To investigate the relationships between species diversity, spatial asynchrony, and ecosystem stability in a spatial context, we simulated landscapes by pooling together M plots that were randomly selected from the same experiment and had the same level of planted richness. These simulated landscapes represented the larger spatial scale (i.e., γ) and were used for deriving diversity and stability across scales. Similar approaches (i.e., randomly aggregating experimental plots) have been used in several recent studies to test the effect of β diversity on ecosystem functioning (Pasari et al. 2013; Mori et al. 2016; van der Plas et al. 2016; Hautier et al. 2018; Ebeling et al. 2020). Specifically, given an experiment and a level of planted richness (e.g., $\alpha_{\text{planted}} = 1$, 2, 4, or 8), there could be 4–48 plots for a single richness level (Appendix S1: Table S1). For each of the 39 experiments and each of the four levels of planted richness, we randomly selected M plots without replacement to create a simulated landscape. This process was repeated until all possible sets of M plots or 1,000 simulated landscapes were obtained (note that different landscapes may share some plots). To generate a reasonable number of landscapes for each experiment and richness level, we omitted combinations of experiment and planted richness that included <7 plots and restricted the landscape size (M) to be no larger than 4 ($M = 2$ or 4 in the main text). With 39 experiments, four levels of planted richness, and two levels of M, we created a total of >77,000 simulated landscapes. Within each simulated landscape, the M plots might have the same, partially overlapping, or completely different species compositions, creating a continuous gradient of β diversity. By simulating landscapes that consist of plots with the same planted richness, we aim to exclude the potential confounding effect of α diversity when testing for β diversity (see Statistical analysis). To examine the robustness of our results, we also simulated landscapes with a higher number of M ($M = 6$) or consisting of adjacent or nonadjacent plots with varying planted richness, which generated qualitatively similar results (see Appendix S1).

Species diversity, spatial asynchrony, and ecosystem stability in simulated landscapes

For each simulated landscape, we calculated species diversity and ecosystem stability at both the plot (α) and landscape (γ) scales. Recent theory suggests that Simpson-based diversity metrics, which account for both species number and the evenness of species abundances, best explain ecosystem stability at different spatial scales (de Mazancourt et al. 2013, Wang and Loreau 2016). Therefore, we measured species diversity using the inverse of the Simpson index, $1/\sum_i p_i^2$, where p_i is the observed relative abundance of species i. Specifically, we defined α diversity (α_D) as the inverse of a weighted average of plot-level Simpson indices, and γ diversity (γ_D) as the inverse of Simpson index at the landscape level (Jost et al. 2007, Wang and Loreau 2016). Plot-level Simpson indices were calculated based on the annual average biomass proportions of species contained in the annual harvests, which were taken from specified areas in each plot, referred to as sampling size (see Appendix S1: Table S1). β diversity (β_D) was calculated as the ratio of γ diversity to α diversity; that is, $\beta_D = \gamma_D/\alpha_D$. Such a multiplicative measure of β diversity represents the compositional turnover between spatial scales (McGlinn et al. 2019) and is consistent with the theoretical framework that we are testing (Wang and Loreau 2016). To test the robustness of our results to the choice of diversity metrics, we also calculated richness-based metrics of α, β, γ diversity, which yielded qualitatively similar results (see Appendix S1).

Spatial asynchrony was defined as

$$\omega = \frac{\left(\sum_i \sqrt{v_{ii}}\right)^2}{\sum_{i,j} v_{ij}},$$

where v_{ij} is the temporal covariance in aboveground productivity between plot i and j (referred to as covariance-based asynchrony; see Loreau and de Mazancourt 2008). This metric accounts for both the correlation among plots and the variance within plots; it varies from

1 (perfect synchrony) to infinity (perfect asynchrony). To test the robustness of our results to the choice of metric, we also used an asynchrony metric defined by one minus the average pairwise correlation in aboveground productivity between plots (referred to as correlation-based asynchrony; see Gross et al. 2013), which also yielded qualitatively similar results (see Appendix S1).

We defined ecosystem stability as the temporal invariability of yearly aboveground biomass productivity (Wang and Loreau 2014, 2016). Specifically, at the landscape scale, we defined γ stability (γ_S) as the reciprocal of the CV^2 (i.e., the ratio of the squared mean to the temporal variance) of landscape ecosystem productivity. At the local scale, we defined α stability (α_S) as the square of the reciprocal of the weighted average plot-level CV. By definition, we have $\gamma_S = \alpha_S \bullet \omega$ (Wang and Loreau 2014). Across all simulated landscapes, the frequency distribution of species diversity and ecosystem stability at different scales are shown in Appendix S1: Fig. S1.

Statistical analysis

We first tested if monoculture plot pairs with different species exhibited on average higher spatial asynchrony than those with the same species. Specifically, for each experiment, we calculated the mean spatial asynchrony for monoculture plot pairs with the same and with different species, respectively, by taking a simple average across plot pairs. We then used a paired *t* test to examine whether spatial asynchrony for monoculture pairs with different species was higher than those with the same species across experiments. Note that in the Jena Experiment, the monoculture plots only had one replicate (Appendix S1: Table S1), and thus we omitted this experiment in this analysis.

We then used linear mixed-effects models to test the relationship between β diversity and spatial asynchrony (ω) at each level of planted richness (α_{planted}) and landscape size (M), with experiment as a random intercept. In doing so, our analyses explicitly accounted for potential confounding effects of α diversity, spatial extent, and any other systematic differences because of differences among experiments (e.g., abiotic factors, species pool, etc.). To evaluate the goodness of model fit, we used the package "MuMIn" to calculate the marginal and conditional R^2, which quantified the proportions of model variation explained by fixed effects (marginal R^2) and the combination of fixed and random effects, respectively (conditional R^2; Nakagawa and Schielzeth 2013). To explore how abiotic and biotic factors may affect the relationship between β diversity and spatial asynchrony, we calculated effect sizes using Fisher's Z:

$$Z = \frac{1}{2}\log\frac{1-r}{1+r},$$

where r is the Pearson correlation coefficient between β diversity and spatial asynchrony (Koricheva et al. 2013). We calculated such an effect size for each level of planted richness (α_{planted}) and landscape size (M) in each experiment and then used linear mixed models to examine how the effect size (Z) is related to both abiotic and biotic factors. Abiotic factors include mean annual temperature (MAT), mean annual precipitation (MAP), and the temporal coefficient of variation of temperature (CV_T) and precipitation (CV_P; data from Craven et al. 2018). Biotic factors include the planted richness (α_{planted}); landscape size (M); the spatial extent, plot size, sampling size, and length of the experiment (see Appendix S1: Table S1).

To quantify the relative importance of α and β diversity in driving γ stability (γ_S), we fitted piecewise structural equation models using the R package 'piecewiseSEM' (Lefcheck 2016). We constructed a structural equation model (SEM) based on predictions by recent theory (Appendix S1: Fig. S2; Wang and Loreau 2016). This model included direct paths from α diversity (α_D) to α stability (α_S), from β diversity (β_D) to spatial asynchrony (ω), and from α stability (α_S) and spatial asynchrony (ω) to γ stability (γ_S). We also included a direct path from α_D to ω, although the direction of this path was predicted to be context dependent (Wang and Loreau 2016). Moreover, to account for effects of unobserved factors, we added correlation errors between α_D and β_D, between α_S and β_D, and between α_S and ω. We used linear mixed-effects models to fit our SEM with experiment as a random intercept. In these analyses, all metrics of diversity, stability, and asynchrony were $\log_{10}$ transformed. Note that the log-transformation made α stability (α_S) and spatial asynchrony (ω) sum up to γ stability (γ_S); that is, $\log_{10}\gamma_S = \log_{10}\alpha_S + \log_{10}\omega$. Consequently, the variance of γ_S was always fully explained by these two components. Our objective with this SEM was to clarify the pathways through which α and β diversity affect γ stability (γ_S) and to quantify their relative importance.

Finally, because many experiments contained data for less than 4 yr (Appendix S1: Table S1), we also tested the robustness of our results to study length. We repeated all the above analyses with five long-term experiments that contained data for at least 10 yr. The R code supporting our results are available upon request.

RESULTS

We first examined whether monoculture plot pairs with different species exhibited higher spatial asynchrony than those with the same species. This special case ($M = 2$, $\alpha_{\text{planted}} = 1$) is a direct test of the underlying mechanism of the stabilizing effect of β diversity; that is, two communities with the same species exhibit more similar population fluctuations than do communities with different species. Overall, monoculture plot pairs with different species exhibited a higher spatial asynchrony than those with the same species (paired *t* test, $P < 0.001$) (Fig. 1). These results were robust to

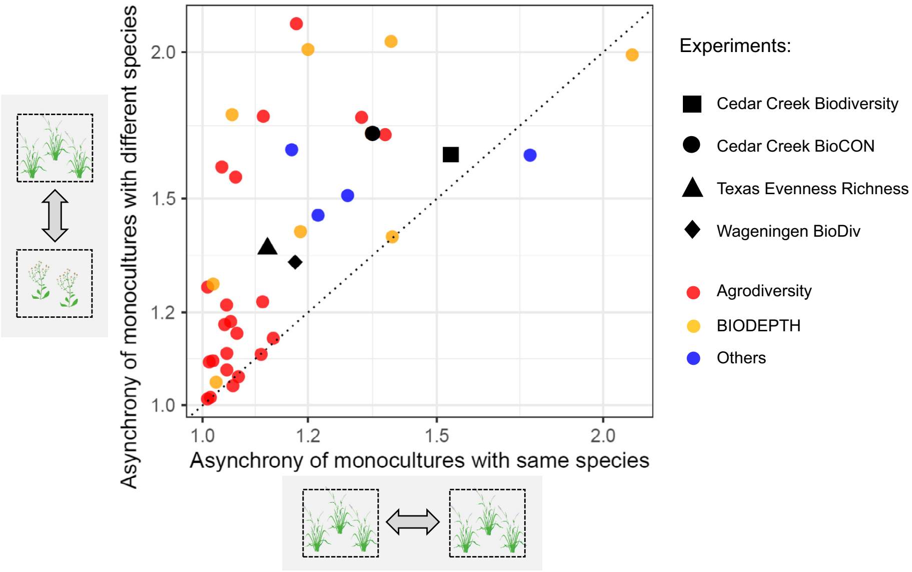

FIG. 1. Spatial asynchrony between monoculture plot pairs with same or different species. Each point represents one experiment, with the *x*-axis showing the average spatial asynchrony for monoculture plot pairs with same species and the *y*-axis the average spatial asynchrony for monoculture plot pairs with different species. The four black points represent four long-term experiments (i.e., ≥10 experiment years). The Jena experiment was excluded from this analysis, because all monocultures have different species. The dashed line denotes a 1:1 line.

different choices of spatial asynchrony metrics (Appendix S1: Fig. S3).

At multiple levels of planted richness ($\alpha_{\text{planted}} = 1, 2, 4, 8$) and landscape size ($M = 2, 4$), we found a significant, positive relationship between spatial asynchrony (ω) and β diversity (β_D) for both Simpson- and richness-based metrics of β diversity and for both covariance- and correlation-based metrics of spatial asynchrony (Fig. 2; Appendix S1: Figs. S4, S5). Their positive relationships were also robust to a larger landscape size ($M = 6$) and whether plots had the same or different planted richness (Appendix S1: Table S2) and were spatially adjacent or not (Appendix S1: Fig. S6). The increased spatial asynchrony in turn led to a higher γ stability (Appendix S1: Fig. S7). Our results also showed that β diversity (β_D) explained a relatively small amount of variation in spatial asynchrony (marginal R^2); a large proportion of this variation was explained by the random effect of experiments (conditional R^2; Fig. 2 and Appendix S1: Figs. S4, S5). Our further analyses showed that the effect size of β diversity on spatial asynchrony increased with the amount (MAP) and variability (CV_P) of precipitation and the sampling size (i.e., harvest area) of the experimental plot, but it was not related to the spatial extent and duration of the experiment, nor to the number and planted richness of plots within simulated landscapes (Table 1).

Using a SEM, we then examined the relative contributions of α and β diversity to γ stability via their effects on α stability (α_S) and spatial asynchrony (ω) (Fig. 3; Appendix S1: Fig. S8). The results show that α diversity (α_D) significantly enhanced α stability, but the fixed effect of α diversity explained a relatively small proportion of variation in α stability (marginal $R^2 = 0.06$). A large amount of variation was explained by the random effect of experiments (conditional $R^2 = 0.65$). Spatial asynchrony (ω) was mainly affected by β diversity and exhibited a weak relationship with α diversity. By definition, on a logarithmic scale, α stability and spatial asynchrony explain all the variation in γ stability, that is, marginal and conditional $R^2 = 1$. We found that the direct effect of α stability on γ stability was more than twice as strong as that of spatial asynchrony, because of a larger variance of α stability across simulated landscapes (i.e., the variance of α stability was five times larger than that of spatial asynchrony). Overall, α diversity had a stronger indirect effect on γ stability (standardized path coefficient of indirect effect: $0.27 \times 0.88 = 0.24$) than did β diversity (standardized path coefficient of indirect effect: $0.18 \times 0.40 = 0.07$; Fig. 3). The stabilizing effects of both α and β diversity also led to a positive diversity–stability relationship at larger scales, where γ stability increased with γ diversity (γ_D; Fig. 4). These relationships were robust to landscape size and different metrics of species diversity (Fig. 4; Appendix S1: Fig. S9).

As most experiments in our data set contained data for a short period of time (mostly 3 yr), we tested the robustness of our results to study length by repeating all our analyses using only the five longest-running experiments (at least 10 yr). The results of these analyses were qualitatively similar to those reported above. The bivariate relationships between spatial asynchrony and β diversity and between γ stability and spatial asynchrony or γ

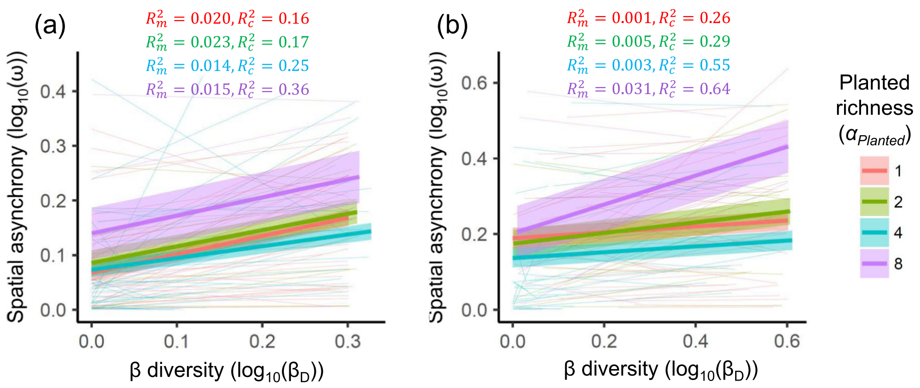

FIG. 2. Relationship between spatial asynchrony (ω) and β diversity (β_D) across simulated landscapes under four levels of planted richness ($\alpha_{planted} = 1, 2, 4$, and 8) and two levels of landscape size: (a) $M = 2$ and (b) $M = 4$. The thick lines represent the overall relationship (fixed effects) at the respective level of $\alpha_{planted}$, and the respective bands represent 95% confidence intervals. The fixed effects of β diversity are all significant ($P < 0.01$). Each thin line represents the least-square regression within each experiment at the respective level of $\alpha_{planted}$. The marginal and conditional R^2 (denoted as $R_m{}^2$ and $R_c{}^2$, respectively) are provided for each level of $\alpha_{planted}$.

TABLE 1. Relationship between the effect size (Fisher Z) of β diversity (β_D) on spatial asynchrony (ω) with abiotic and biotic factors. The effect size was calculated for both covariance- and correlation-based spatial asynchrony. For across-site variables, the model is $Z = \text{MAT} + \text{MAP} + \text{CV}_T + \text{CV}_P + S_E + S_P + S_S + L$, with $\alpha_{planted}$ and M as random effects. For within-site variables (e.g., $\alpha_{planted}$ and M), the model is: $Z = \alpha_{planted} + M$, with experimental site as the random effect. Significant coefficients are indicated in bold ($P < 0.05$).

	Effect size of β_D on covariance-based ω		Effect size of β_D on correlation-based ω	
Abiotic and biotic factors	Coefficient	P value	Coefficient	P value
Across-site variables				
Mean annual temperature (MAT)	0.002	0.52	0.006	0.10
Mean annual precipitation (MAP)	**10^{-4}**	**0.00**	**2×10^{-4}**	**0.00**
CV of annual temperature (CV_T)	0.002	0.53	0.003	0.23
CV of annual precipitation (CV_P)	**0.006**	**0.00**	**0.004**	**0.00**
Spatial extent of the experiment (S_E)	-4×10^{-7}	0.57	-10^{-6}	0.31
Plot size within the experiment (S_P)	2×10^{-4}	0.34	2×10^{-4}	0.29
Sample size within the plot (S_S)	**0.006**	**0.02**	**0.007**	**0.00**
Length of the experiment (L)	0.005	0.25	0.007	0.13
Within-site variables				
Planted richness ($\alpha_{planted}$)	-10^{-4}	0.98	0.005	0.16
Landscape size (M)	−0.014	0.07	−0.004	0.59

diversity were generally positive, although the explanatory power of the fixed effects varied depending on planted richness, landscape size, and the diversity and asynchrony metrics (Fig. 4 and Appendix S1: Figs. S4, S5, S8, S9). In SEMs using only data from long-term experiments, our general conclusion remained the same, but α diversity had a stronger direct positive effect on α stability, and β diversity had a weaker direct positive effect on spatial asynchrony when compared with the results using data from all experiments (Appendix S1: Fig. S8).

DISCUSSION

Our study provides a rigorous test of the prediction from recent theory that β diversity contributes to stabilizing ecosystem functioning at larger scales by increasing spatial asynchrony (Wang and Loreau 2016). By simulating landscapes within grassland experiments that controlled for initial α diversity ($\alpha_{planted}$), species pool, spatial scale, and environmental conditions, our test excludes potential confounding effects of biotic and abiotic factors. Our approach, therefore, provides a test of the unique effect of β diversity on ecosystem stability. In particular, by controlling for initial α diversity, our test of the effect of β diversity is similar to real-world ecosystems with constant local diversity and decreasing β diversity, which reflect the homogenizing impacts of land-use change, climate change, and biological invasions (Dornelas et al. 2014, Magurran et al. 2015, Blowes et al. 2019). The similarity is not complete because we usually cannot determine the initial α

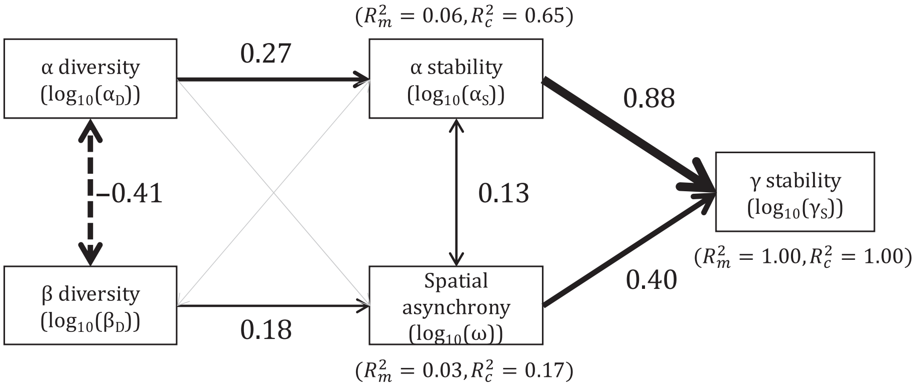

FIG. 3. Structural equation model (SEM) depicting the pathways of α and β diversity in regulating landscape ecosystem stability (γ_S), through its two components: α stability (α_S) and spatial asynchrony (ω). Uni- and bidirectional arrows represent a direct effect and correlation between variables, respectively. Black solid and dashed arrows indicate significant positive and negative relationships ($P < 0.05$), respectively, and numbers on the arrows represent the standardized path coefficients. Gray arrows indicate nonsignificant relationships. The marginal and conditional R^2 (denoted as R_m^2 and R_c^2, respectively) for α stability, spatial asynchrony, and γ stability are provided. Model test statistics are: Fisher's $C = 0.992$, df = 4, and $P = 0.91$. In this SEM, species diversity is measured using Simpson-based metrics and landscape size is 2.

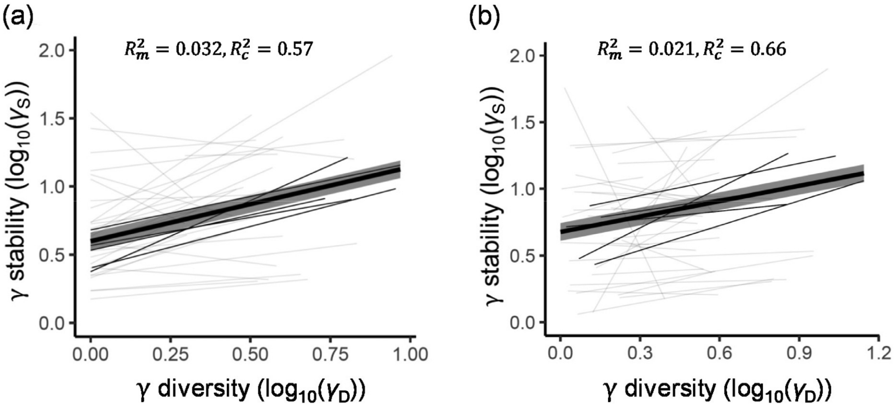

FIG. 4. Relationship between γ stability (γ_S) and γ diversity (γ_D): (a) $M = 2$, (b) $M = 4$. The thick black lines represent the overall relationship (fixed effect), and the respective bands represent 95% confidence intervals. The fixed effects are both significant ($P < 0.01$). Each thin line represents the least-square regression within each experiment, with the dark color indicating five long-term experiments (i.e., ≥10 experiment years). The marginal and conditional R^2 (denoted as $R_m{}^2$ and $R_c{}^2$, respectively) are provided. Species diversity is measured by Simpson-based metrics.

diversity, that is, species pool, for real-world ecosystems. However, using the realized α diversity (α_D) as explanatory variable in our analysis we accounted for this difference between diversity measures.

We found that β diversity increased spatial asynchrony, which in turn increased γ stability. This result was consistent across levels of planted richness, landscape sizes, study lengths, and species diversity and spatial asynchrony metrics (Figs. 2, 3; Appendix S1: Figs. S4–S7). Our results, therefore, suggest that biotic homogenization destabilizes ecosystem productivity at larger scales, and thus processes that maintain high spatial turnover of species in heterogeneous landscapes are important (Thompson et al. 2015). Our analyses exhibit considerable variation among experiments in the magnitude, and occasionally the direction, of the relationship between β diversity and spatial asynchrony (Fig. 2; Appendix S1: Figs. S4, S5), which suggests that their relationship is context dependent. We found that the effect size of β diversity on spatial asynchrony increased with the amount and variability of precipitation (Table 1), coinciding with recent findings that the stabilizing effect of biodiversity in naturally assembled grasslands increases along a precipitation gradient (Hallett et al. 2014), as long as aridity is not too extreme where it can reverse the relationship (Wang et al. 2020). Future experiments are required to test the context dependence of β diversity in regulating ecosystem stability.

In a spatial context, larger-scale biodiversity (γ_D) and stability (γ_S) can both be partitioned into a local scale (α_D or α_S) and a spatial transition component (β_D or ω) (Jost 2007, Wang and Loreau 2016). Theory predicts that diversity and stability are related to each other at all these spatial scales (Wang and Loreau 2016). Our SEM provides the first experimental, quantitative test of this cross-scale framework and highlights the different pathways through which α and β diversity affect ecosystem stability at larger scales. Specifically, α diversity increases α stability and β diversity increases spatial asynchrony (ω), both of which contribute to enhancing ecosystem stability at larger scales (Fig. 4; Appendix S1: Fig. S8). The stabilizing effects of these biodiversity components generate positive diversity–stability relationships at the landscape scale (Fig. 4). Taken together, our results imply that both local biodiversity and spatial turnover of species should be preserved to maintain ecosystem stability at larger spatial scales.

Our results also show that α diversity had stronger effects than β diversity on the γ stability of ecosystem productivity, a pattern that was robust to diversity metrics and landscape sizes and was more pronounced in long-term studies (Fig. 4; Appendix S1: Fig. S8). The stabilizing effect of α diversity agrees with previous findings that species diversity is an important driver of local ecosystem stability (Tilman et al. 2014, Isbell et al. 2015, Craven et al. 2018; but see Blüthgen et al. 2016). The weaker effect of β diversity might be due to the small sampling size (0.1–19 m^2) and the relatively low heterogeneity of environmental conditions given the small spatial extent (up to 10 ha) of the experiments in our study (Appendix S1: Tables S1 and S2; Grace et al. 2016). Given the small sampling size, demographic stochasticity can be pronounced (de Mazancourt et al. 2013), which decreases the spatial correlation of population dynamics (Engen et al. 2005, Wang et al. 2017). Under these conditions, the positive effect of β diversity on spatial asynchrony is expected to be weak (Table 1; see also Wang and Loreau 2016). Moreover, the relatively homogenous environmental conditions result in low variation in spatial asynchrony across simulated landscapes, and thus cause a weaker effect of spatial asynchrony on γ stability compared to α stability (comparing the effect size of spatial asynchrony among different landscape size M in Appendix S1: Fig. S8). In this respect, our use of data from experiments, where the environmental heterogeneity was minimal and dispersal between plots was prevented by weeding, allowed for a particularly restrictive test of the hypothesis that β diversity per se already could increase spatial asynchrony and thus landscape stability.

With respect to further upscaling across space and across levels of ecological organization (Gonzalez et al. 2020), these conditions of relatively small spatial scale as well as the restricted environmental heterogeneity and dispersal in our analyses should be extended in future research. We anticipate that β diversity may have a stronger stabilizing effect across larger landscape areas (e.g., hundreds to thousands of hectares), with increased spatial heterogeneity (Grace et al. 2016) and increased potential for biotic and abiotic exchange between landscape units (Oehri et al. 2020), where the effect of demographic stochasticity should be weak. At even larger spatial scales, for example, regional, continental, and global scales, however, the effect of β diversity might weaken because spatially decoupled environmental fluctuations provide sufficiently strong stabilizing effects on ecosystem functioning (Barton et al. 2013, Wang and Loreau 2016). Such a hypothesis is supported by our preliminary analysis by simulating landscapes across sites over Europe, which covered a broader range of environmental heterogeneity and species pool and exhibits a weak positive relationship between β diversity and spatial asynchrony (Appendix S1: Fig. S10). Because our simulated landscapes and the experiments studied did not account for dispersal, an important spatial process in natural ecosystems that may interact with β diversity by providing influxes of new species for local communities was not represented in our analysis (Mellin et al. 2014). Although dispersal could occur in the experiments, it was rarely quantified and typically reduced by weeding that was performed to maintain the originally designed species compositions (Appendix S1: Table S1). It is thus largely unknown how much dispersal matters in such experimental systems. Future experiments should manipulate both β diversity and dispersal across large gradients of spatial heterogeneity in large-scale landscapes (e.g., McGranahan et al. 2016, Germain et al. 2017) to assess the robustness of the present findings for real-world landscapes relevant for decision makers and conservation management.

Our study, based on 39 grassland biodiversity experiments across North America and Europe, provides a comprehensive and rigorous test of theory on the joint effects of α and β diversity on ecosystem stability across spatial scales. Our results reveal that both components of diversity enhance stability at larger spatial scales, and we anticipate that the effects—particularly those of β diversity—will strengthen at scales relevant for conservation and management. In light of ongoing land-use change at different spatial scales (Meyfroidt et al. 2018) and globally consistent trends of increasing biotic homogenization (Magurran et al. 2015), we recommend a cross-scale approach to maintaining the benefits of biodiversity over time that conserves both local diversity and heterogeneity within a landscape.

ACKNOWLEDGMENTS

We thank Shahid Naeem and anonymous reviewers for helpful comments, and Maowei Liang for help with Fig. 1. This work was supported by the National Natural Science Foundation of China (31988102), the National Key Research and Development Program of China (2017YFC0503906), and the CAS Interdisciplinary Innovation Team (JCTD-2018-06), and is a product of the sTability group funded by sDiv (www.idiv.de/stability), the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118). The Jena experiment is funded by the German Research Foundation (DFG; FOR 1451). The biodiversity experiments at Cedar Creek are funded by the U.S. National Science Foundation's Long-Term Ecological Research (LTER; DEB-1234162), Long-Term Research in Environmental Biology (DEB-1753859), Major Research Instrumentation (DBI-

1725683), and Ecosystem Sciences (NSF DEB-1120064) Programs. The data set Hector_UK was funded by the Natural Environmental Research Council Centre for Population Biology and National Science Foundation grants DEB-0080754 and INT-9725937. The Texas MEND study was funded by US-NSF DEB-0639417 and USDA-NIFA-2014-67003-22067. ML and CdM were supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41) and by the BIOSTASES Advanced Grant and the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement 666971). FI acknowledges support from the LTER Network Communications Office (DEB-1545288). JC was supported by the International Research Training Group TreeDì funded by the German Research Foundation (DFG), 319936945/GRK2324 and BS by the University Research Priority Program for Global Change and Biodiversity of the University of Zurich. SW, DC, and ML conceived research; CB, JC, JD, DHD, NE, AH, AJ, JK, VL, JL, HWP, PBR, JVR, DT, BW, and BS contributed data; SW, DC ML, CDM, and FI performed research and analyzed data; SW wrote the first draft; and all co-authors contributed substantially to revisions.

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