

LETTER

Predicting ecosystem stability from community composition and biodiversity

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Abstract

As biodiversity is declining at an unprecedented rate, an important current scientific challenge is to understand and predict the consequences of biodiversity loss. Here, we develop a theory that predicts the temporal variability of community biomass from the properties of individual component species in monoculture. Our theory shows that biodiversity stabilises ecosystems through three main mechanisms: (1) asynchrony in species' responses to environmental fluctuations, (2) reduced demographic stochasticity due to overyielding in species mixtures and (3) reduced observation error (including spatial and sampling variability). Parameterised with empirical data from four long-term grassland biodiversity experiments, our prediction explained 22–75% of the observed variability, and captured much of the effect of species richness. Richness stabilised communities mainly by increasing community biomass and reducing the strength of demographic stochasticity. Our approach calls for a re-evaluation of the mechanisms explaining the effects of biodiversity on ecosystem stability.

Keywords

Biodiversity, demographic stochasticity, environmental stochasticity, overyielding, prediction, stability.

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INTRODUCTION

Ecosystems are subject to temporal variations in environmental conditions and various stressors, and an important aspect of their functioning is their temporal stability in response to these extrinsic factors. The intuitive idea that biodiversity allows different species to compensate for each other and thereby stabilises communities and ecosystems (MacArthur 1955; Elton 1958) was challenged by theoretical work in the 1970s (May 1973), leading to a long-standing debate on the relationship between diversity and stability in ecology (McNaughton 1977; McCann 2000; Ives & Carpenter 2007; Loreau 2010, p. 124). This debate can be partly resolved by the fact that diversity often has a dual effect on stability: it stabilises total community biomass, while at the same time destabilising individual species abundances (Tilman 1996; Tilman *et al.* 2006; Roscher *et al.* 2011). Many experiments have confirmed the stabilising effects of biodiversity on ecosystem properties (Hooper *et al.* 2005; Tilman *et al.* 2006; van Ruijven & Berendse 2007; Isbell *et al.* 2009; Hector *et al.* 2010; Proulx *et al.* 2010; Allan *et al.* 2011).

A number of theories have been developed recently to explain the stabilising effect of diversity on aggregate ecosystem properties. These theories have followed four main approaches (Loreau 2010,

p. 128): (1) a statistical approach based on the phenomenological mean–variance scaling relationship, which considers neither population dynamics nor species interactions explicitly but which is easily applied to empirical data (Doak *et al.* 1998; Tilman 1999); (2) a stochastic, dynamical approach that describes population dynamical responses to environmental fluctuations but does not explicitly consider species interactions (Yachi & Loreau 1999); (3) a general population dynamical approach that includes a deterministic component describing species interactions and a stochastic component describing environmental fluctuations (Hughes & Roughgarden 1998, 2000; Ives *et al.* 1999; Ives & Hughes 2002); and (4) specific models of interspecific competition in which trade-offs lead to coexistence (Tilman 1999; Lehman & Tilman 2000). Although each of these approaches sheds some light on the effects of species diversity on ecosystem stability, the underlying mechanisms that drive these effects have not been elucidated and remain contentious (Loreau 2010, ch. 5). So far, none of these approaches has been able to predict ecosystem stability from the properties of component species.

Here, we expand previous theory following the population dynamical approach (Ives *et al.* 1999; Lehman & Tilman 2000; Loreau & de Mazancourt 2008) to more realistic communities in which species are affected by a combination of intra- and interspe-

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cific competition, environmental stochasticity and demographic stochasticity, and in which they differ in all their parameters. We use this new theory to generate a prediction of ecosystem stability that is derived from the properties of individual species in monoculture and that can be applied to mixed communities. We then test our theoretical prediction with the results of four long-term grassland biodiversity experiments in which species richness was manipulated, and we discuss how it can elucidate the mechanisms that drive the effects of diversity, in particular species richness, on ecosystem stability.

THEORETICAL MODEL

Materials and methods

Our theoretical model is based on a discrete-time version of the classical Lotka–Volterra model that incorporates environmental and demographic stochasticity (Ives *et al.* 1999; Loreau & de Mazancourt 2008):

$$\tilde{r}_i(t) = \ln \tilde{N}_i(t+1) - \ln \tilde{N}_i(t) = r_{mi} \left[1 - \frac{\tilde{N}_i(t) + \sum_{j \neq i} \alpha_{ij} \tilde{N}_j(t)}{K_i} \right] + \sigma_{ei} u_{ei}(t) + \frac{\sigma_{di} u_{di}(t)}{\sqrt{\tilde{N}_i(t)}}, \quad (1)$$

where $\tilde{N}_i(t)$ is the biomass of species i in year t , and $\tilde{r}_i(t)$ is its instantaneous mass-specific growth rate in year t . A tilde denotes the real, unknown quantities, as observed biomass and growth rate are affected by observation error (see below). r_{mi} is species i 's intrinsic (maximum) rate of natural increase, K_i is its carrying capacity and α_{ij} is the interspecific competition coefficient describing the effect of species j on species i . Environmental stochasticity describes a year effect on a species' growth rate. It is incorporated through $\sigma_{ei} u_{ei}(t)$, where σ_{ei}^2 is the environmental variance, and $u_{ei}(t)$ are normal variables with zero mean and unit variance that are independent through time (white noise) but may be correlated between species (e.g. a good year for one species may be good for another species as well). Demographic stochasticity is the last term in Equation (1). It is due to variation in birth and death rates between individuals or independent reproductive units. Here, we incorporate it in the form of the first order, normal approximation that is traditionally used in the theory of stochastic population dynamics (Lande *et al.* 2003) to facilitate mathematical analysis. Individuals are not well defined in grassland plants and the number of individuals (such as the number of genets) is a poor descriptor of plant population dynamics. The number relevant for population dynamics is the number of plant modules, defined as demographic plant units with a high functional independence (e.g. tillers, shoots or rosettes, Schmid 1990). Module density is quite strongly correlated with biomass (Marquard *et al.* 2009), which is why we use biomass rather than number of individuals. σ_{di}^2 is the demographic variance, and $u_{di}(t)$ are independent normal variables with zero mean and unit variance. The observed biomass of species i in year t , $N_i(t)$, is estimated through a sampling procedure that generates an observation error due to factors such as spatial heterogeneity and variability in sample collection and sorting. Observed biomass is the real biomass plus a random variable representing observation error on a log scale, $\frac{\sigma_{oi} u_{oi}(t)}{\tilde{N}_i(t)}$ (Ives *et al.* 2003), where σ_{oi}^2 is the observation variance, and $u_{oi}(t)$ is the average of independent normal variables with zero

mean and unit variance across the subsamples taken in a plot in year t :

$$\ln(N_i(t)) = \ln(\tilde{N}_i(t)) + \sigma_{oi} \overline{u_{oi}(t)}. \quad (2)$$

Community biomass is defined as the sum of the biomasses of component species. We use our model to derive an analytical prediction of the temporal coefficient of variation of community biomass, as this inverse measure of ecosystem stability has been commonly used in experiments (Tilman *et al.* 2006; Ives & Carpenter 2007; van Ruijven & Berendse 2007; Isbell *et al.* 2009; Proulx *et al.* 2010; Allan *et al.* 2011). The derivation proceeds as follows. First, we compute the deterministic equilibrium values of model (1) in the absence of any stochasticity. Second, we assume that the system reaches a stationary state, and we linearise Equations (1) and (2) around the equilibrium by representing all forms of stochasticity as additive Gaussian variables. Third, we derive an analytical prediction of the variance-covariance matrix of component species biomasses. Fourth, we obtain the variance of community biomass as the sum of the variances and covariances of component species biomasses, from which we obtain the coefficient of variation of community biomass (see more details in Online Supporting Information, section A).

The analytical predictions of the observed variance and coefficient of variation (CV) of community biomass at stationary state should hold as a first order, linear approximation for any more realistic model (Online Supporting Information, section A). This approximation, however, is impractical because estimating the large number of pairwise competition coefficients between species would require longer time-series than available. Given the data limitations, we make the simplifying assumption that interspecific competition affects only the mean abundances of species, not their year-to-year dynamics, that is, the abundance of species in a given year does not predict its effect on competitors in the following year (Online Supporting Information, section A). This simplifying assumption allows us to derive a simple theoretical prediction for the CV of community biomass that can be parameterised using existing experimental data. Our prediction can be seen as a first, coarse approximation; longer time-series would be required to estimate competitive effects. If competitive effects could be estimated, the full first-order approximation could be computed by solving equation (A11). We test our prediction against simulations where species differ in all their parameters, with high and asymmetric competition in the following.

Results

Our prediction is

$$CV_{NT}^2 = \left(\frac{\sigma_{NT}}{\bar{N}_T} \right)^2 \approx \varphi_e \Sigma_e^2 + \frac{\Sigma_d^2}{\bar{N}_T} + \lambda \frac{\Sigma_o^2}{n_x} \quad (3)$$

In this equation, φ_e is a measure of the synchrony of species environmental responses, where species environmental responses are species-specific properties independent of species interactions and measured by the year effect on their growth rate in monocultures; synchrony is then computed from the variance-covariance matrix of these environmental responses. Σ_e^2 is the mean scaled environmental variance, Σ_d^2 is the mean scaled demographic variance, \bar{N}_T is mean community biomass, λ is Simpson's (1949) concentration index (a measure of dominance), n_x is the number of subsamples taken

within a plot and year used to estimate the CV of community biomass and Σ_o^2 is the mean observation variance (Online Supporting Information, section A, equations A22–A26).

Equation (3) comprises three additive terms, which encapsulate the respective influences of environmental stochasticity, demographic stochasticity and observation error on variability of total biomass. The mean scaled environmental, mean scaled demographic, and mean observation variances are weighted means of individual-level variances. As such they can be affected by differences in community composition and species relative abundances across plots. However, there should be no systematic effect of species diversity on these variances unless there is selection for species with high or low variances in mixtures (Loreau & Hector 2001). Equation (3) then suggests three main mechanisms through which species diversity can stabilise community biomass: (1) by decreasing the synchrony of species environmental responses, ϕ_o , which dampens the effect of environmental stochasticity at the community level through functional compensation between species (Gonzalez & Loreau 2009; Loreau 2010, p. 130); this mechanism underlies the insurance hypothesis, (2) by increasing community biomass, N_T , which increases the number of demographic modules and thereby reduces the strength of demographic stochasticity at the community level and (3) by decreasing Simpson's concentration index, λ , which reduces the impact of observation error at the community level. Observation error probably results mainly from spatial heterogeneity and sampling variability, whose effects tend to average out at the community level.

NUMERICAL SIMULATIONS

Materials and methods

We first tested the accuracy of our simplified analytical prediction (3) with numerical simulations of model (1) in which species differed in all their parameters and there was no observation error. In the simulations, we considered four cases by varying two factors: (1) the relative strength of environmental stochasticity vs. demographic stochasticity (two levels, in which species demographic and environmental standard deviations were drawn from different ranges), and (2) connectance, that is, the proportion of species competing with each other (two levels). In low-connectance communities, coexistence was ensured by setting most competition coefficients to zero, resulting in low levels of interspecific competition overall. In high-connectance communities, all species competed with each other and coexistence was ensured by a low variability among competition coefficients scaled (divided) by relative carrying capacities (Jansen & Kokkoris 2003), resulting in higher levels of interspecific competition than in low-connectance communities.

For numerical simulations, we drew parameters from random distributions to generate stable coexisting communities at 6 species richness levels ($S = 1, 2, 4, 8, 16, 32$) and 11 target values of the synchrony of species environmental responses, ϕ_o , as our analysis above shows that this is a key factor that affects ecosystem stability. Our measure of synchrony is bounded between 0 (perfect asynchrony) and 1 (perfect synchrony). Community dynamics was simulated for 2010 time-steps, and realised communities were those where none of the species went extinct during the simulation. The last 10 time-steps ensured that no species was on the brink of extinction at the end of the time-series, and time-steps 1000–2000

were used to estimate the characteristics of the community and of its component species. We simulated 1000 single-species communities. For each of the other values of species richness, we generated 200 realised communities for each target level of species synchrony of environmental response (11 values regularly spaced between 0 and 1). We repeated the simulations for two levels of connectance and two levels of environmental and demographic variances. More details are provided in Online Supporting Information, section B1.

Results

Numerical simulations strongly supported our analytical prediction at low levels of connectance as there was an excellent match between the prediction and the realised CV of community biomass at all levels of species diversity (Fig. 1, left panels). At high levels of connectance and interspecific competition, the match was still present but was less strong (Fig. 1, right panels). Recall that our prediction includes the effect of interspecific competition on average species abundances, but not its effect on year-to-year dynamics. Although the strength of interspecific competition should not affect community variability when communities are symmetrical (Ives *et al.* 2000; Loreau 2010, p. 150), it does when species differ (Fowler 2009; Loreau & de Mazancourt 2013). Our prediction then tends to underestimate community variability, suggesting that asymmetric competition tends to destabilise communities (Loreau & de Mazancourt 2013).

Our theory predicts that the relative importance of the various stabilising mechanisms at work depends on the relative strengths of environmental stochasticity, demographic stochasticity and observation error because the three terms are additive (Equation 3). When environmental stochasticity is the dominant force driving community dynamics, asynchrony between species environmental responses (mechanism 1 above) is responsible for the stabilising effect of diversity (Fig. S1, top panels). In contrast, when demographic stochasticity dominates, diversity affects stability through its effect on community biomass (mechanism 2 above; Fig. S2, bottom panels).

APPLICATION TO FIELD DATA

Materials and methods

One attractive feature of our approach is that it can be applied directly to empirical data. All species-specific parameters, such as their intrinsic rate of natural increase, carrying capacity, environmental response through time and demographic variance, can be estimated using replicated monoculture time-series for each species. Observation variance requires measurements of several samples within monoculture plots. The only information needed from mixtures is the time-average of the abundance of each component species (Online Supporting Information, section B3). Equation (3) can then be used to predict the variability of community biomass in mixtures from independent data.

We used data from four long-term grassland biodiversity experiments in Cedar Creek (Minnesota, USA), Jena (Germany), Texas (USA) and Wageningen (The Netherlands) to assess the extent to which our prediction matched the observed temporal variation of community biomass (Online Supporting Information, section B2–B4). In all experiments, diversity treatments were maintained for at least 8 years through hand-weeding programs. More details are pro-

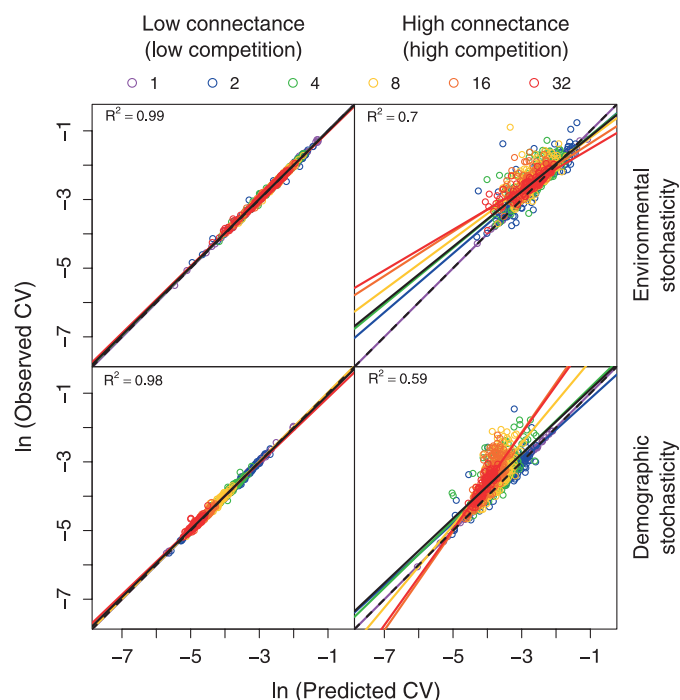


Figure 1 The coefficient of variation (CV) of community biomass is well explained by the prediction in simulated model communities. Left column: low-connectance (low competition) communities; right column: high-connectance (high competition) communities. Either environmental stochasticity (top row) or demographic stochasticity (bottom row) is the main driver of community variability. Each dot represents one community, colour indicates species richness. A sample of 1200 of the 12 000 simulated communities was plotted for clarity. Dashed black line represents the 1 : 1 line. Coloured solid lines represent the regression lines for each corresponding level of species richness. Black solid line is the regression line pooling all levels of species richness together, regression whose R^2 is shown.

vided in Online Supporting Information, section B2 and summarised in Table S1.

For each data set, species parameters were estimated for each species independently, using time-series analysis of log biomass and growth rates in replicated monocultures. Several samples within monoculture plots were taken in Cedar Creek and Jena; observation variance could thus be estimated for these two experiments. Parameters from component species were then combined into the compo-

nents of our prediction (Equation 3), with weightings depending on their mean abundance in mixture (Online Supporting Information equations A22–A26). Details are provided in Online Supporting Information, section B3. Major axis regression was performed where explanatory variables were estimated, with the *lmodel2* package in R 2.11.1 (see Online Supporting Information, section B4).

To understand the importance of the different mechanisms in predicting community variability and the effect of species richness, we developed two sets of structural equation models (Online Supporting Information, section B5). Structural equation modelling allows evaluation of complex causal hypotheses by translating a set of hypothesised causal relationships into a pattern of expected statistical relationships in the data (Grace 2006). The first set of models simply related observed variability to the three additive components of our prediction, demographic stochasticity, environmental stochasticity and observation error, for the four data sets (Fig. 2). The second set of models was designed to address the more complex question of how each of the six individual components of Equation (3) contributed to the overall effect of species richness on variability in community biomass (Fig. 2).

Results

Across the four data sets, our prediction explained 22–75% of the variance in the observed CV of aboveground community biomass (Fig. 3). Our prediction fared in a similar way than species richness in Cedar Creek, Wageningen and Jena, and much better in Texas (Table 1). When the two variables were fitted together, both variables were significant (Table 1). The explanatory power, compared to our prediction alone, increased minimally with the addition of species richness in Cedar Creek and Texas, and moderately so in Wageningen and Jena (Table 1). Regression lines between observed CV of aboveground biomass and our prediction were often away from the 1 : 1 line.

To understand how the three additive components of our prediction (Equation 3) contribute to its explanatory power, we modelled their respective effects on observed variability using structural equation modelling (Fig. 4). In this analysis, the three components were treated as equal and separate (though intercorrelated) predictors. Since the intercorrelation strengths among them were modest (0.06–0.34), it is possible to interpret the standardised path coefficients, which technically represent predicted sensitivities, as measures of their relative importance. Demographic stochasticity was the most

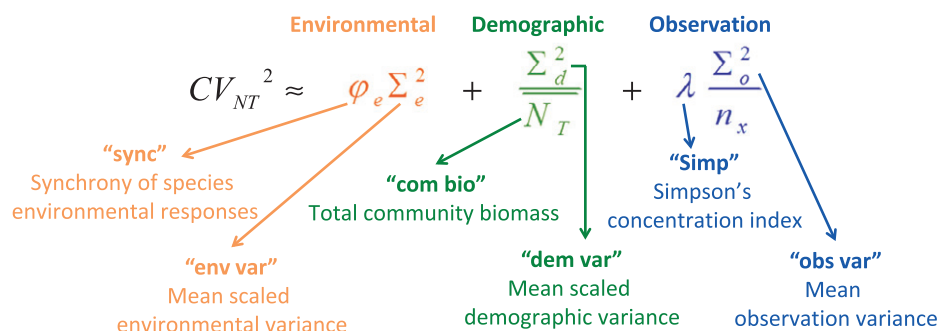


Figure 2 Decomposing Equation 3 for structural equation modelling. In the first set of structural equation models (Fig. 4), the prediction was decomposed into three additive terms, that is, environmental (orange), demographic (green) and observation (blue) terms. In the second set of structural equation models (Fig. 5), it was decomposed into the six components shown below the equation.

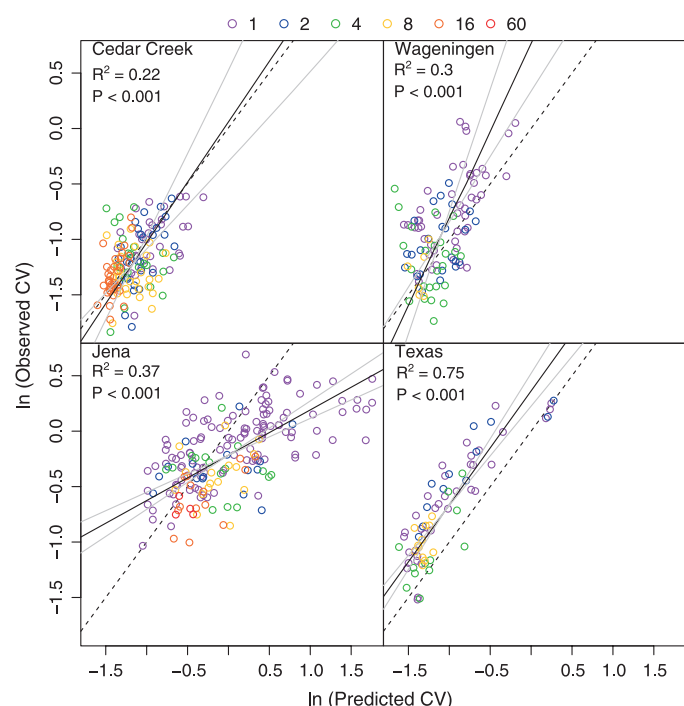


Figure 3 The observed coefficient of variation (CV) of community biomass in the four experiments was relatively well predicted by the prediction. R^2 and P -values are for major axis regressions (Supplementary Information section B4). Black dashed lines indicate 1 : 1 relationship. Grey lines indicate 95% confidence interval for slope. Colours indicate the number of planted or sown species.

Table 1 Fractions of the variance (R^2) of the CV of community biomass among plots explained by our prediction alone (Equation 3), planted or sown species richness alone, and both variables on a log scale: $\log(\text{observed CV}) \sim \log(\text{term})$

| | Whole prediction only | Species Richness only | Whole prediction + Species Richness |
|-------------|-----------------------|-----------------------|-------------------------------------|
| Cedar Creek | 0.22*** | 0.19*** | 0.26*** |
| Wageningen | 0.30*** | 0.29*** | 0.41*** |
| Jena | 0.37*** | 0.25*** | 0.49*** |
| Texas | 0.75*** | 0.13** | 0.77*** |

Stars indicate level of significance: *** $P < 0.001$, ** $P < 0.01$. Note that for each site, the model including the whole prediction only has the same number of degrees of freedom as the model with species richness only: both have one single, continuous explanatory variable. Statistics for the full model (whole prediction + species richness) are presented in Appendix Table S3.

important component in three experiments (Wageningen, Jena and Texas); environmental stochasticity also made a significant contribution in these experiments (Fig. 4). Unexpectedly, predicted observation error was the most important component at Cedar Creek. This effect of observation error is confirmed by a direct fit of measured observation error on the observed CV of community biomass, which was also significant (Cedar Creek, $R^2 = 0.1$, $P < 0.001$; Jena $R^2 = 0.18$, $P < 0.001$). Correlations among components were generally positive. A negative correlation between demographic and environmental stochasticities was observed for Cedar Creek (Fig. 4).

Next, we used structural equation modelling to investigate which components of equation (3) were likely to have contributed to the

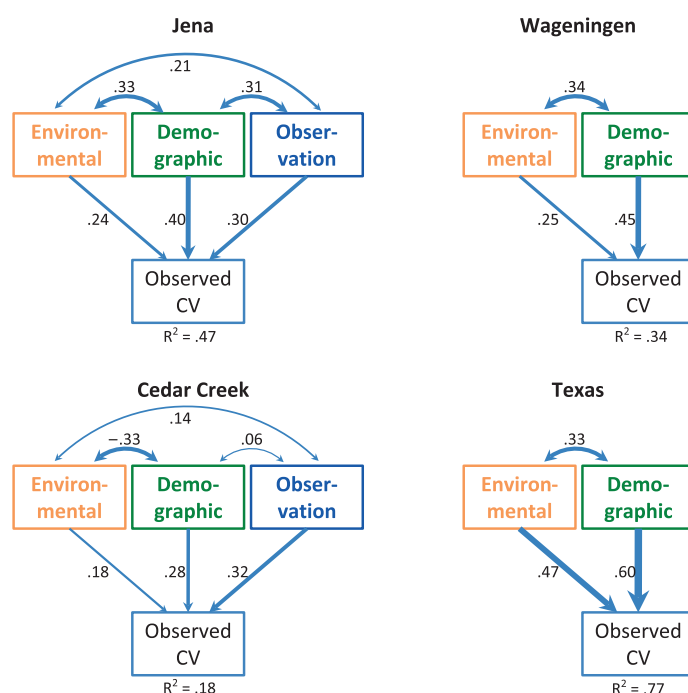


Figure 4 SEM standardised results showing the contribution of each of the three terms of our prediction (Fig. 2) to the observed coefficient of variation of community biomass (Obs. CV). Env. term: environmental stochasticity term $\phi_e \Sigma_e^2$; Dem. term: demographic stochasticity term $\frac{\Sigma_d^2}{N_T}$; Obs. term: observation error term λ_{obs}^2 . There is no estimate for observation error in Wageningen and Texas, where samples are always taken at the same place and represent the quasi-totality or the totality of plots; therefore, there is no error due to partial sampling and spatial heterogeneity. Standardised path coefficients represent predicted sensitivities, that is, what the predicted responses would be if an individual predictor were varied while the other variables in the model were held constant (Grace & Bollen 2005).

stabilising effect of species richness on community biomass. We first consider the effect of species richness on each component. Theory predicts that synchrony of species environmental responses, mean community biomass and Simpson's concentration index should be affected by species diversity, and they always were (Fig. 5). The mean scaled environmental, scaled demographic and observation variances represent weighted means of individual-level variances; they depend on community composition and species relative abundances but we expect no systematic effect of species richness on these variances unless there is selection for species with either high or low variances in mixtures. These variances were indeed not affected by species richness most of the time, with three exceptions: demographic variance increased with species richness in Cedar Creek and Texas, and observation variance increased with species richness in Cedar Creek. There was thus a selection effect for more variable species in these two experiments.

The effect of species richness on community variability was mediated through community biomass in all experiments (Fig. 5). Additional effects of species richness were observed directly (in Wageningen) or through variables that are highly correlated with species richness, such as Simpson's concentration index (in Cedar Creek and Jena), or synchrony (Texas). In both Cedar Creek and Texas, the stabilising effect of diversity was slightly counteracted by a selection effect for species with higher demographic variances.

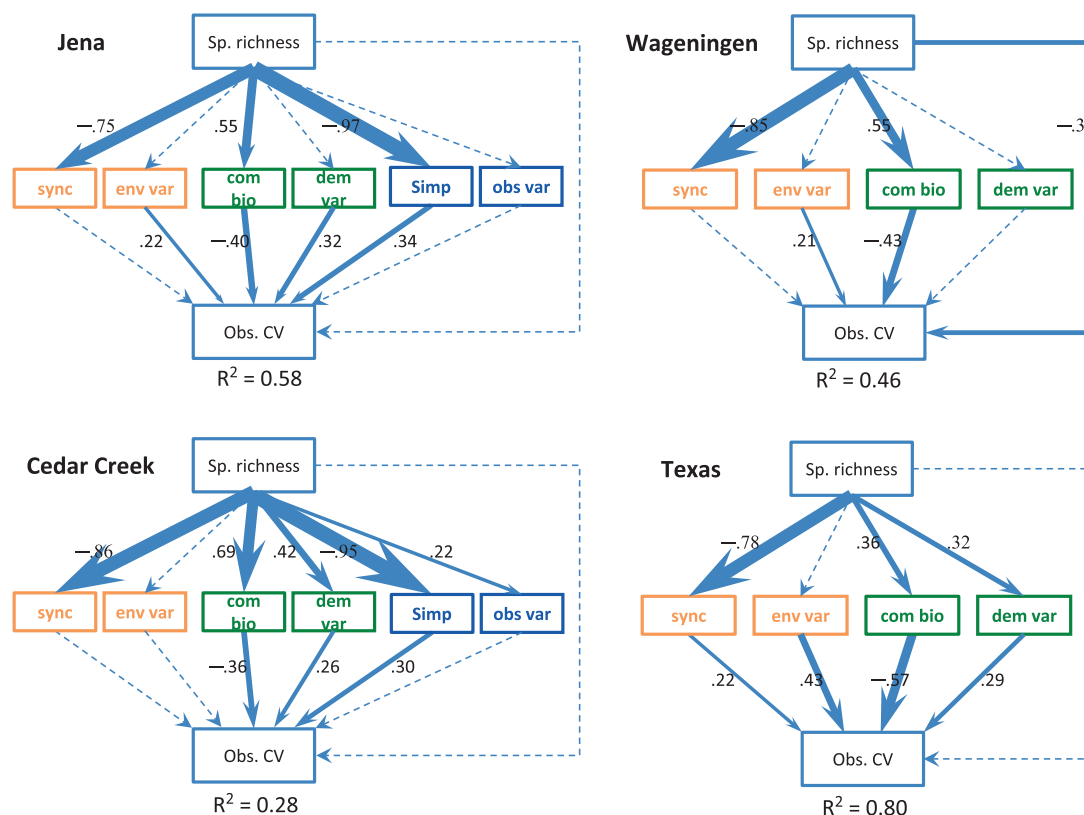


Figure 5 Structural Equation Modelling standardised results showing how planted or sown species richness (Sp. richness) affected the observed CV (coefficient of variation of community biomass, Obs. CV) through each of the six components of our prediction (Fig. 2). Sync: synchrony of species environmental responses ϕ_e ; env var: mean scaled environmental variance Σ_e^2 ; com bio: mean community biomass \bar{N}_T ; dem var: mean scaled demographic variance Σ_d^2 ; Simp: Simpson's (1949) concentration index, λ ; obs var: mean observation variance Σ_o^2 . Coefficients as in Fig. 4.

The first stabilisation mechanism we identified is reduced environmental stochasticity at the community level because of differences between species' responses to environmental fluctuations, which generate decreased synchrony ϕ_e with increased diversity. A strong negative effect of species richness on the synchrony of species environmental responses was found in all four experiments (Fig. 5). Surprisingly, the significant effect of species richness on the synchrony of species environmental responses (ϕ_e) only seemed to make a significant contribution to community stability in Texas (Fig. 5).

The second mechanism is reduced demographic stochasticity at the community level because of increased community biomass with higher diversity. In all four experiments, more diverse communities had a higher mean community biomass (Fig. 5). This second stabilisation mechanism is likely to have played a significant role in all four experiments, where community biomass made a significant contribution to community stability. However, in Cedar Creek and Texas, this was slightly counteracted by a selection effect of more variable species (Fig. 5). This is shown by the positive effect of species richness on demographic variance, which in turn results in higher community variability.

Finally, we predicted a possible effect of diversity on community stability through reduced observation error. This seemed to be the case in the two experiments in which multiple samples per plot were taken, that is, Cedar Creek and Jena (Fig. 4), where the effect was mediated through Simpson's concentration index (Fig. 5). In

both experiments, the predicted observation error was significantly correlated with its observed value (Online Supporting Information, Fig. S3). Species richness also slightly affected the measured observation error (Cedar Creek: $R^2 = 0.08$, $P < 0.001$; Jena: $R^2 = 0.02$, $P < 0.05$). Thus, observation error is likely to have played a minor role in the positive relationships between biodiversity and stability in these experiments.

DISCUSSION

The theory we have developed here makes three major contributions: first, it clarifies the nature of a number of stabilising mechanisms and how they interact to drive ecosystem stability; second, for the first time it provides a way to disentangle them quantitatively in field biodiversity experiments; and third, it provides the first prediction of the stability of aggregate ecosystem properties from the properties of individual species. Our theoretical prediction encapsulated in Equation (3) explained 22–75% of the variance in the observed variability of aboveground community biomass in four long-term grassland biodiversity experiments. The percent of variance explained by our prediction was similar to that explained by planted species richness alone, except in Texas where it was much better (Table 1). Adding species richness to a model with our prediction improved explanatory power little in two experiments (Cedar Creek and Texas), and moderately in two locations (Jena and Wageningen) (Table 1). This suggests that the mechanisms captured in

our prediction cover a good part of the effects of species richness on community variability. Our prediction also includes some effects of total plot biomass, evenness and species identity that come into play in the various terms of Equation (3). Although our prediction was correlated with the observed CV, it could be further improved to increase its predictive ability.

Note that a correlation between our prediction and the observed CV could be expected for monocultures since both are estimated from the same data. However, correlations remained highly significant when monocultures were removed from the analysis, except in Wageningen where it became non significant (results not shown). Many different factors could account for the lower range of explanatory power of our theoretical prediction. First, time-series are short (in terms of time-series analysis), and there is a relatively low number of monocultures. Accuracy in parameter estimation is therefore limited, especially because field data are very variable. Second, our prediction assumes that the abundance of species in a given year does not affect their competitors the following year. As discussed previously, longer time-series would be required to obtain reliable estimates of yearly competition effects, and a better prediction using estimated competition coefficients could be compiled solving equation (A11). Third, our prediction relies on a first-order, linear approximation of yearly competitive effects and stochasticity terms; it assumes that perturbations are small – which they are not, and that interactions between these various factors are negligible, or in other words, that the behaviour in monoculture reflects the behaviour in mixture. Finally, experiments are probably far from the steady-state assumed.

Our theory predicts that three main mechanisms underlie the stabilising effect of species richness on community biomass in biodiversity experiments. The first mechanism, asynchrony of species environmental responses, is predicted to be important when environmental stochasticity plays a significant role in community variability (Fig. S1, top row). The strong negative correlation between the synchrony of species environmental responses and species richness in all four experiments (Fig. 5) shows that this stabilisation mechanism is potentially strong. This potential, however, seemed to be realised only in Texas, the only experiment where synchrony of species environmental responses made a significant contribution to community variability (Fig. 5). The relatively short length of the experiments (8–13 years) and variability between plots may also have restricted our ability to detect significant environmental signals in the data.

Note that a species' environmental response is an intrinsic species-specific property that defines its functional response type or trait (Diaz & Cabido 2001); it is measured by the year effect on growth in monoculture, in the absence of interspecific interactions. It can also be estimated from natural systems with replicated time-series (Mutshinda *et al.* 2009; Thibaut *et al.* 2012). In contrast, population fluctuations result from many different processes, including species responses to the environment, density dependence, species interactions, and demographic stochasticity. Therefore, asynchrony in species environmental responses must be carefully distinguished from asynchrony in population fluctuations (Loreau & de Mazancourt 2008). In particular, asynchrony in species environmental responses cannot be measured by the summed covariances of population fluctuations. Summed species covariances are strongly affected by species interactions such as competition, and can be negative even when competition acts to decrease community stabil-

ity (Loreau & de Mazancourt 2013). Therefore, summed species covariances are unlikely to provide a mechanistic explanation for community stability. In contrast, asynchrony of species environmental responses is a measure of functional response diversity (Diaz & Cabido 2001); it is the basic mechanism of the insurance hypothesis (Ives *et al.* 1999; Yachi & Loreau 1999). It is also the likely cause of the stabilising effect of diversity on community biomass in resource competition models (Tilman 1999; Lehman & Tilman 2000). In these models, the interspecific trade-offs that generate coexistence, such as species having different optimal temperatures, also cause species to have asynchronous responses to environmental (temperature) fluctuations. Our theory highlights asynchrony of species environmental responses as a mechanism that drives the stabilising effect of species diversity on aggregate ecosystem properties, a mechanism that is more closely related to the concept of functional compensation as initially envisaged by ecosystem ecologists (McNaughton 1977). Thibaut *et al.* (2012) found that this was likely the main mechanism driving the diversity-stability relationship in coral reefs communities. We suggest that future research on compensatory dynamics would benefit from focusing on asynchrony of species environmental responses rather than on mere patterns of population fluctuations (Loreau 2010, ch. 5).

The second mechanism our theory highlights, reduced demographic stochasticity with increased community biomass, is predicted to be important when demographic stochasticity is a significant driver of community variability (Fig. S2, bottom row). Species richness increases community biomass through functional complementarity between species and/or through selection of more productive species, a phenomenon known as overyielding (Loreau & Hector 2001). A positive effect of species richness on community stability through community biomass was found in all four experiments (Fig. 5). This stabilisation mechanism played a role in all four experiments, although it was slightly counteracted by a selection effect for more variable species in Cedar Creek and Texas (Fig. 5).

Our analysis provides a mechanistic underpinning for the stabilising effect of community biomass. Previous arguments were based on empirical scaling relationships between the mean and the variance of species abundances with the form, $\sigma_{mi}^2 = an_i^z$ where z is a scaling coefficient typically between 1 and 2 (Taylor & Woivod 1982). Two known mechanisms create such a scaling coefficient for individual species: demographic stochasticity (Anderson *et al.* 1982), and competitive interactions between species (Kilpatrick & Ives 2003). Both mechanisms were at work in our model, although only demographic stochasticity results in a stabilisation of diverse communities through overyielding. We suggest that future research would benefit from exploring the role of demographic stochasticity to explain ecosystem stability.

Finally, our theory also predicts a potential effect of diversity on ecosystem stability through reduced observation error. This effect comes from the assumption that the biomasses of different species are measured independently. The higher the diversity, the more the observation errors on species biomass average out in community biomass. Common species contribute more to community biomass variability than rare species, with the appropriate weighting being given by Simpson's index. Observed observation error decreased slightly with species richness in the field, although the R^2 were small (results section). Is reduced observation error a genuine stabilisation

mechanism or just a methodological problem? We suspect that a significant part of measurement error comes from spatial heterogeneity. If biodiversity decreases spatial heterogeneity at the community level by averaging out heterogeneity of the component species, then it can be considered a genuine mechanism through which diversity stabilises communities. This mechanism was likely to play a role in the Cedar Creek and Jena experiments (Fig. 4 and 5). Although reduced observation error may be viewed as a statistical mechanism due to sampling constraints rather than as a genuine ecological mechanism, its influence on the results of biodiversity experiments should not be ignored. Observation error, which has been overlooked so far, will be important to consider explicitly in future biodiversity experiments.

What is the role of competition in stabilising communities? Inter-specific competition is often hypothesised to stabilise communities through compensatory dynamics. However, mathematical exploration of the full community dynamics, obtained by solving equation (A11) for a 2-species community with interspecific competition, shows that interspecific competition can have dual effects, but that it most often has a destabilising effect at both the population and community levels (Loreau & de Mazancourt 2013). Some recent studies suggest that interspecific interactions contribute little to community stability in a range of animal taxa (Mutshinda *et al.* 2009; Almaraz *et al.* 2012; Thibaut *et al.* 2012). Although our prediction encompasses the effect of interspecific competition on average abundance, it ignores its potential effects on year-to-year dynamics. Longer time-series will be necessary to assess the importance of year-to-year interspecific competitive interactions in experimental plant communities.

Our work provides a new predictive theory of the stability of community biomass that can be parameterised from species-specific properties obtained independently, and their abundance in mixture. To be estimated, our prediction requires experimental data from monocultures, but given enough temporal and spatial resolution, parameters could in principle be estimated from natural communities (as in Almaraz *et al.* 2012; Thibaut *et al.* 2012). Thus, our approach offers the potential for understanding and predicting the stability of an important ecosystem service in the face of biodiversity loss and other environmental changes from knowledge of individual species responses to these changes. This could provide a useful tool to inform policy and economic decision-making processes about the insurance value of biodiversity in the provision of ecosystem services (Baumgärtner 2007).

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AUTHOR CONTRIBUTIONS

CdM and ML designed and analysed the theoretical model, with help from BH. CdM performed the simulations, derived the approximation and method for parameter estimation, with help

from ML, BH, BS and FI. FB, EDL, HWP, CR, BS, DT, JvR, AW and BJW provided, and FI and AL analysed the data. JBG performed structural equation modelling. All authors contributed to writing the manuscript.

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