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General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding

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Abstract. Insurance effects of biodiversity can stabilize the functioning of multispecies ecosystems against environmental variability when differential species' responses lead to asynchronous population dynamics. When responses are not perfectly positively correlated, declines in some populations are compensated by increases in others, smoothing variability in ecosystem productivity. This variance reduction effect of biodiversity is analogous to the risk-spreading benefits of diverse investment portfolios in financial markets.

We use data from the BIODEPTH network of grassland biodiversity experiments to perform a general test for stabilizing effects of plant diversity on the temporal variability of individual species, functional groups, and aggregate communities. We tested three potential mechanisms: reduction of temporal variability through population asynchrony; enhancement of long-term average performance through positive selection effects; and increases in the temporal mean due to overyielding.

Our results support a stabilizing effect of diversity on the temporal variability of grassland aboveground annual net primary production through two mechanisms. Two-species communities with greater population asynchrony were more stable in their average production over time due to compensatory fluctuations. Overyielding also stabilized productivity by increasing levels of average biomass production relative to temporal variability. However, there was no evidence for a performance-enhancing effect on the temporal mean through positive selection effects. In combination with previous work, our results suggest that stabilizing effects of diversity on community productivity through population asynchrony and overyielding appear to be general in grassland ecosystems.

Key words: *BIODEPTH project; biodiversity; ecosystem functioning; insurance effect; overyielding; stability.*

Introduction

One value of biodiversity to humans is its potential to buffer ecosystem processes like productivity against environmental variation. This insurance value of biodiversity consists of a variance reduction effect and a performance enhancing effect on the temporal mean (Yachi and Loreau 1999). Buffering effects of biodiversity have usually been considered in the context of

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fluctuations over time but could also apply to spatial environmental variation (Loreau et al. 2003). The variance reduction effect of biodiversity on productivity has been likened to the risk-spreading benefits of diverse portfolios of investments in financial markets leading to the closely related concepts of the portfolio and statistical averaging effects (Doak et al. 1998, Tilman et al. 1998, Lehman and Tilman 2000). Variance reduction effects require only that fluctuations in the populations of a guild of species are not perfectly synchronized, because under perfect synchrony an entire guild or trophic level would effectively behave as one species. In contrast, when species responses are not perfectly positively correlated, declines in some species can be compensated by increases in others and the averaging of their asynchronous population fluctuations reduces the variability of the collective productivity of the aggregate community and ecosystem (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999). This asynchrony through differential species responses can be interpreted as a form of temporal niche differentiation (Loreau 2000). The degree of population asynchrony could also be affected by species interactions like competition (Tilman et al. 1998, Lehman and Tilman 2000). The performance-enhancing component of the insurance effect occurs when positive selection effects lead to dominance of species with better-than-average monoculture performance increasing the long-term average (Yachi and Loreau 1999). Additional stabilizing effects of biodiversity can also result from overyielding when complementary mixtures of species perform better than expected and increase mean levels of ecosystem functioning relative to the variability.

A recent meta-analysis of 44 biodiversity experiments (Cardinale et al. 2007) found that selection effects accounted for only one third of the net effect. Moreover, they were often negative. This suggests that the performance-enhancing effect of positive selection may not contribute strongly to any insurance effect. In contrast, two-thirds of the biodiversity effects were due to complementarity (Cardinale et al. 2007) suggesting that overyielding may play a greater role in generating temporal stability than previously thought: none of the current theory formally considers performance-enhancing effects of overyielding on the temporal mean.

One potentially confusing aspect of these buffering effects is that diversity can have a stabilizing effect on aggregate community or ecosystem properties (like primary productivity) at the same time that it has a destabilizing effect on the populations of the constituent species through interactions with greater numbers of species (Tilman 1996). These simultaneous stabilizing and destabilizing effect at different levels may partly explain why mixed effects of diversity have been reported during the decades of research on the relationship between diversity and stability (Ives and Carpenter 2007). The most recent review of stability in biodiversity experiments reported that while two grassland biodiversity experiments have found stabilizing effects of plant diversity on net primary production, only two of five single-trophic level microcosm experiments did (Griffin et al. 2009).

Previous analyses of stability in biodiversity experiments have used negative summed covariances to quantify competitive interactions between species (Tilman et al. 1998, Lehman and Tilman 2000, Valone and Hoffman 2003, Steiner et al. 2005). These analyses have failed to find that negative covariances are stronger in diverse communities and concluded that competitive interactions play little or no role in generating insurance or portfolio effects of diversity. However, Loreau and De Mazancourt (2008) have shown that negative covariances cannot be used as indicators of compensatory competitive interactions in multispecies communities for the following reason. First, imagine a community of two species interacting over time under fluctuating conditions that sometimes favor one species and sometimes the other. Strong competition will lead to negative temporal covariance (or correlation) in the abundances of the two species: when one is competitively superior its abundance will be high and that of the other species low and vice versa. Now consider adding a third species; it can strongly negatively covary with one of the two species but not both since a negative correlation with one species inevitably leads to a positive correlation with the other. As more species are added to the community this effect becomes more widespread and the average correlation between species tends to zero despite strong competition. New methods for identifying the contribution of species interactions to community stability are under development (Loreau and de Mazancourt 2008) but will require more detailed information and longer time series than we currently possess in our data set.

In this paper, we provide the first general experimental test for temporal insurance effects of diversity within a single trophic level (grassland plant communities) using the BIODEPTH network of coordinated biodiversity experiments conducted at eight European field sites. We show that the productivity of more diverse communities was generally more stable over time due to the variance reduction effect of population asynchrony and to increases in the temporal mean relative to the temporal variability produced by complementarity and overyielding.

METHODS

Data

The analyses presented use data on net aboveground biomass production ($g \cdot m^{-2} \cdot yr^{-1}$) of species from the experimental plots at each of the eight BIODEPTH fieldsites for the three main years of the project (Spehn et al. 2005). The data set comprises information on 480 plots each containing between one and 32 species (and between one and three plant functioning groups, namely, grasses, legumes, and other forbs). In total, this produces 1934 data points per year, with each data point reporting the biomass of a species in an individual plot. Each monoculture or species mixture was replicated in two identical plots (with a few exceptions: five plant assemblages were replicated four times, see Spehn et al. 2005).

To standardize fluctuations relative to changes in mean productivity over time, we quantified variability as the coefficient of variation (CV) where CV is the ratio of the standard deviation, s, to the mean, m, expressed as a percentage:

$$\mathrm{CV} = (\sigma/\mu) \times 100.$$

Since a decrease in the CV can result from an increase in the mean, a decrease in the variance (SD), or both, we examine patterns in all three statistics.

Temporal CVs were calculated for the biomass of individual species, for functional groups and for aggregate communities (ecosystem aboveground annual net primary production) over the first three years of the BIODEPTH experiment (longer time series exist for some sites that show similar patterns as long as weeding is maintained; Pfisterer et al. 2004). Overyielding will have a stabilizing effect (reduced CV) when diversity increases the ratio of the mean relative to the standard deviation. Spatial CVs were also calculated for the biomass of individual species, functional groups and the experimental communities they composed. However, as there was no effect of diversity on spatial variability and as there is a clear danger that we could publish a false-negative result due to the reduction of spatial heterogeneity at our field sites during establishment we present the results only shortly in the Appendix A.

Analysis

Since our design includes fixed and random effects we used mixed-effects analysis using the lme function from the nlme package (Pinheiro and Bates 2000) for R 2.10.1 (R Development Core Team 2009). Readers not familiar with mixed-effects models can think of them as a maximum likelihood-based form of ANOVA that is the recommended approach for analysis of mixed-model designs that include fixed and random effects (Bolker et al. 2009). Mixed-effects models use restricted maximum likelihood (REML) to estimate regression intercepts and slopes or treatment means (generally, "intercepts") for fixed-effect explanatory variables (e.g., treatments) and to predict the variability (variance components) of slopes or intercepts for random effects (e.g., sites and blocks). Following the BIODEPTH experimental design and our a priori hypotheses, our analysis treats diversity (sown species richness) and organizational level (individual species, functional group or aggregate community) as fixed effects, reporting their point estimates with 95% confidence intervals. Sites were treated as random effects, allowing both the intercepts and slopes of the regression slopes vs. diversity to vary with location. Species compositions were also treated as a random effect (nested within sites). The fixed-effect component of our models therefore examined the effects of diversity, level and their interaction. For the random-effect component of our models we followed a model building strategy (Pinheiro and Bates 2000) that uses likelihood ratio tests of models with and without a given random effect to determine which show significant levels of variation and are required in the model. The likelihood ratio test is based on the change in deviance (≈sums of squares) due to the removal of the random effect that is omitted from the reduced model. The change in deviance approximately follows a χ^2 distribution with the appropriate degrees of freedom and the test tends to be conservative (Pinheiro and Bates 2000). Variance components for the random effects are reported as standard deviations (that is the square root of the variance component) to be on the same scale as the original measurements. To calculate the evenness between experimental and reference plots we used the reciprocal Simpson's index divided by the number of species by plot (Magurran 2003) by replacing number of species with biomass of species per plot. All intervals are 95% confidence intervals unless otherwise stated.

RESULTS

Temporal stability

The effect of diversity on temporal variability (temporal CV) differed depending on organizational level ($\log_2$[species richness] × level interaction; $F_{2,2684} = 80.9$, $P < 0.001$; Fig. 1). As hypothesized, diversity had a stabilizing effect on variability at the community level as shown by the significant negative effect on the temporal CV (slope vs. $\log_2$[species richness] with 95% CI = −5.2 [−9.3 to −1.2]; Fig. 1, left). In contrast, the effect of diversity on the population CVs was significantly positive and therefore destabilizing (slope = 11.1 [7.5–14.6]; Fig. 1, right). At the intermediate functional group level there was no effect on average (slope = 1.4 [−2.3–5.2]; Fig. 1, center). Since the population, group and community CVs are derived from the same plot they may not be strictly independent. However, a supplementary analysis where each plot was used to give a CV for one level only produced the same results (Appendix B, Appendix C).

There was significant variation around these average slopes from site to site (likelihood ratio test: $\chi^2_1 = 10.6$, $P = 0.005$; standard deviation of the variation in slopes across sites = 4.0 [1.9–8.6]) (Fig. 1, colored lines and points; Appendix D). The strength of the relationship at different sites ranged from 0.16 to 0.46 when quantified using pseudo-R^2 (the correlation coefficients for observed vs. predicted values from the mixed-effects model; Appendix E). There was also significant variation in the temporal CVs of different species compositions within diversity levels ($\chi^2_1 = 181.6$, $P < 0.001$; SD of the variation in means for different compositions = 15.8 [13.6–18.3]).

The temporal CV is the temporal mean divided by the temporal standard deviation (expressed as a percentage).

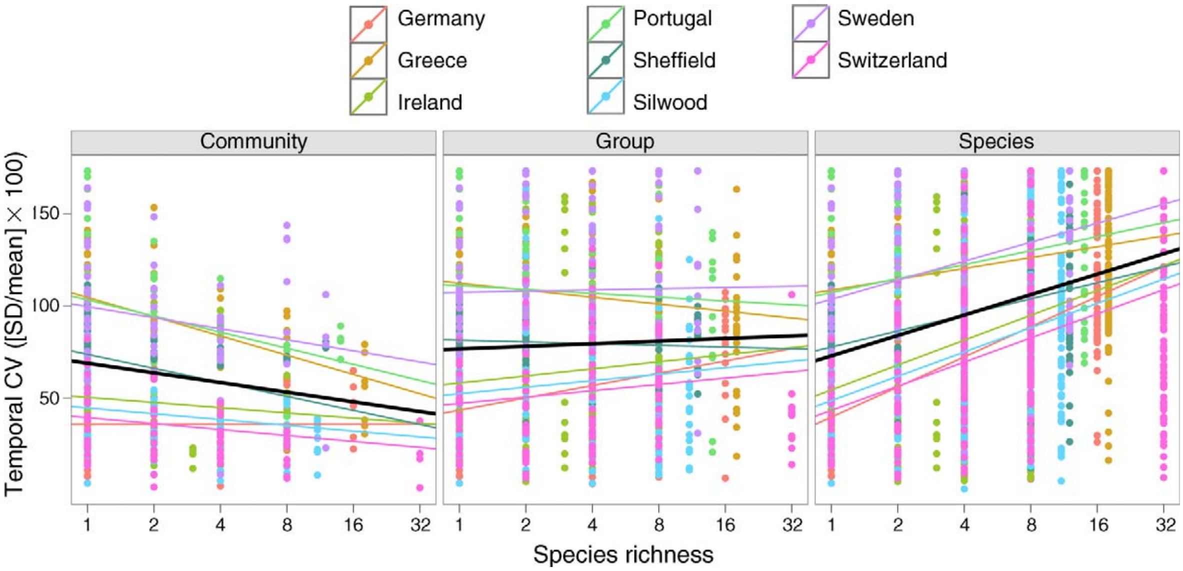

FIG. 1. Temporal CVs of aboveground net primary production (colored points) as a function of diversity for individual species, functional groups, and aggregate communities. Solid black lines are the fixed-effect linear regression slopes for the overall response per level from the mixed-effects model, while colored points and lines show the significant random effects variation for sites (see Supplement for individual site patterns). Note the $\log_2$ scale of the *x*-axis.

Therefore, lower variability can come about as a function of an increasing mean, decreasing SD, or both. Net annual aboveground biomass production is positively related to diversity at all of the eight BIODEPTH sites except Greece (Hector et al. 1999, Spehn et al. 2005). An examination of the mean–SD relationships (Appendix F) showed that variability generally declined relative to the increasing mean except in Greece (Appendix G).

Stability and overyielding

To complement the relative measure of variability given by the CV, we used Loreau's (1998) $\bar{D}$, as a relative measure of overyielding that quantifies the deviation of mixtures yields from the null expectation of the weighted average of the monoculture yields of the constituent species. We analyzed the temporal CVs for the aggregate community level as a function of mean overyielding averaged over the same three-year period (taking the natural log, after adding one to remove zeros, to get a more even distribution). We found a significant negative relationship between temporal variability (CV) and overyielding (slope with 95% CI = –6.9 [–13.2 to –0.5]; Fig. 2) which is consistent with a stabilizing effect. There was substantial and significant variation across sites ($\chi^2_1 = 85.0$, $P < 0001$; standard deviation of the intercepts for different sites = 29.9 [17.2–51.8]) but the variation in the slopes was not significant (parallel colored lines in Fig. 2; $\chi^2_1 = 1.0$, $P = 0.6$, SD = 4.4 [0.6–32.4]). Within sites there was also significant variation in the variability of different species compositions (χ^2_1 = 12.4, P = 0.004; SD of the means for different species compositions within sites and species richness levels = 12.1 [8.6–16.9]).

Stability and temporal asynchrony of species populations

We examined the correlations between pairs of species in the two-species mixtures only since, as explained in the introduction, the average correlation tends to zero as species richness increases. Our analysis confirmed a stabilizing effect of population asynchrony since two-species communities composed of pairs with more negative temporal correlations had lower community temporal CVs (slope = 11.2 [5.6–16.9]; Fig. 3). There was significant variation in the intercepts of this relationship at the different sites ($\chi^2_1 = 41.9$, $P < 0.0001$; SD of the regression intercepts for individual sites = 27.1 [15.6–47.1]), but not in their slopes ($\chi^2_1 = 3.1$, $P = 0.22$, SD = 9.0 [3.1–25.8]), as well as substantial within-site variation between different species compositions ($\chi^2_1 = 4.36$, P = 0.036, SD = 9.0 [4.3–18.5]). Sadly, with our current data we are not able to say how much of this stabilizing effect of population asynchrony is due to intrinsic differential responses to temporal variation and how much is due to competition between species under the changing conditions.

Stability and mean performance enhancement through positive selection effects

We found no significant relationship between the temporal CVs and the selection effects. This provides no support for the performance-enhancing component of the insurance effect, that is increases in the long-term mean through dominance by species with higher-than-average monoculture yields (Appendix H).

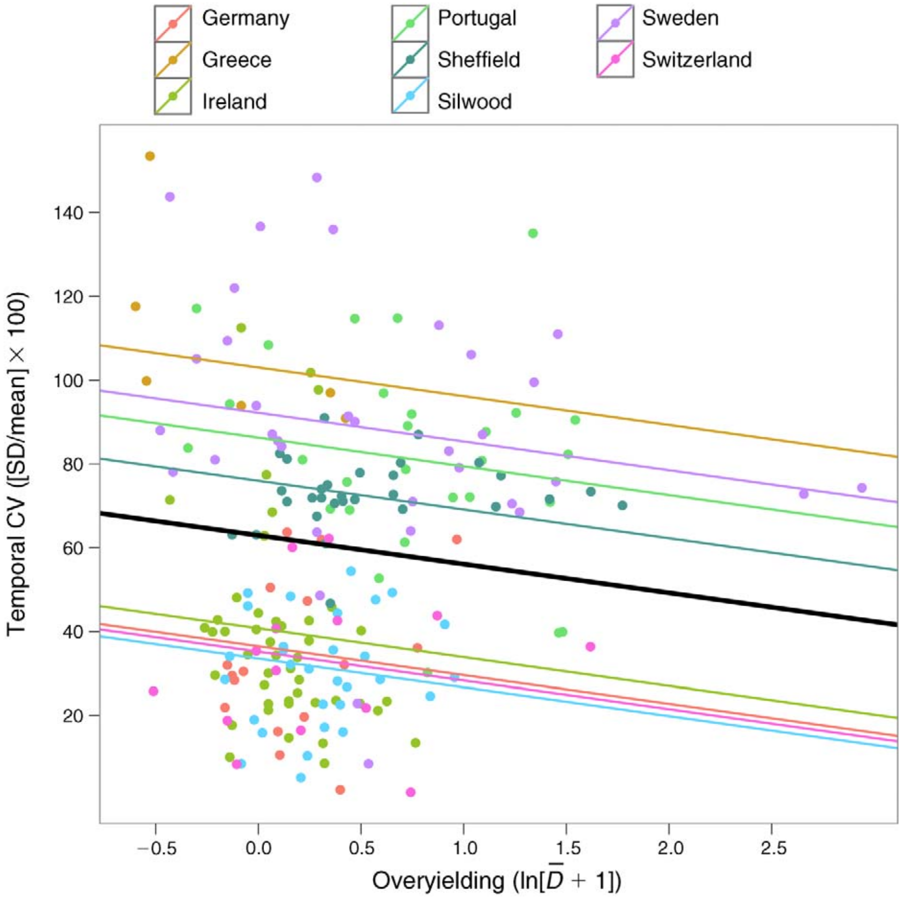

FIG. 2. Temporal variability (CV) of aggregate community biomass as a function of overyielding ($\bar{D}$, averaged over three years, natural-log-transformed after adding 1). The black line is the significantly negative linear regression slope (the fixed effect for overyielding) from the mixed-effects model reported in the results, and the colored points and lines indicate the variability in the relationship across sites (the random intercepts for the overyielding relationship at different sites).

DISCUSSION

Our results support both a destabilizing effect of diversity on the variability of individual populations and a stabilizing effect on ecosystem net primary production. This contrast between stabilizing and destabilizing effects of diversity depending on the organizational level provides experimental agreement with the results of other grassland biodiversity experiments (Tilman et al. 2006, van Ruijven and Berendse 2007) and an analysis of long-term observational field data from Inner Mongolia grasslands (Bai et al. 2004). In our analysis, the effects of diversity on the variability of individual functional groups lay midway between its stabilizing effects on aggregate communities and destabilizing effects on individual populations. This result shows that the averaging effect of asynchronous fluctuations of individual functional groups is weaker than that of individual species. To put it another way, the stabilizing insurance effects of diversity were not provided by functional groups alone: there is substantial stabilizing asynchrony in the fluctuations of species within functional groups in addition to the asynchrony of the groups themselves. However, it is important to remember that our groups were intended as functional effects groups (that is species expected to have similar effects on ecosystem functioning) and not functional response groups (species expected to respond in a similar way to environmental perturbation).

Our analysis of the stabilizing effect of diversity at the community level demonstrated significant but modest effects of two proposed mechanisms but no effect of a third. Although there was substantial variability between- and within-sites we found stabilizing effects through variance reduction (population asynchrony or statistical averaging) and mean performance enhancement. However, enhancement of temporal mean performance was due to overyielding and not positive selection effects. Theory needs to incorporate these stabilizing effects of overyielding through the performance enhancement effect. For the reasons explained above our analysis of asynchrony was restricted to two-species mixtures and deeper investigation of these effects requires longer time series and new analytical methods

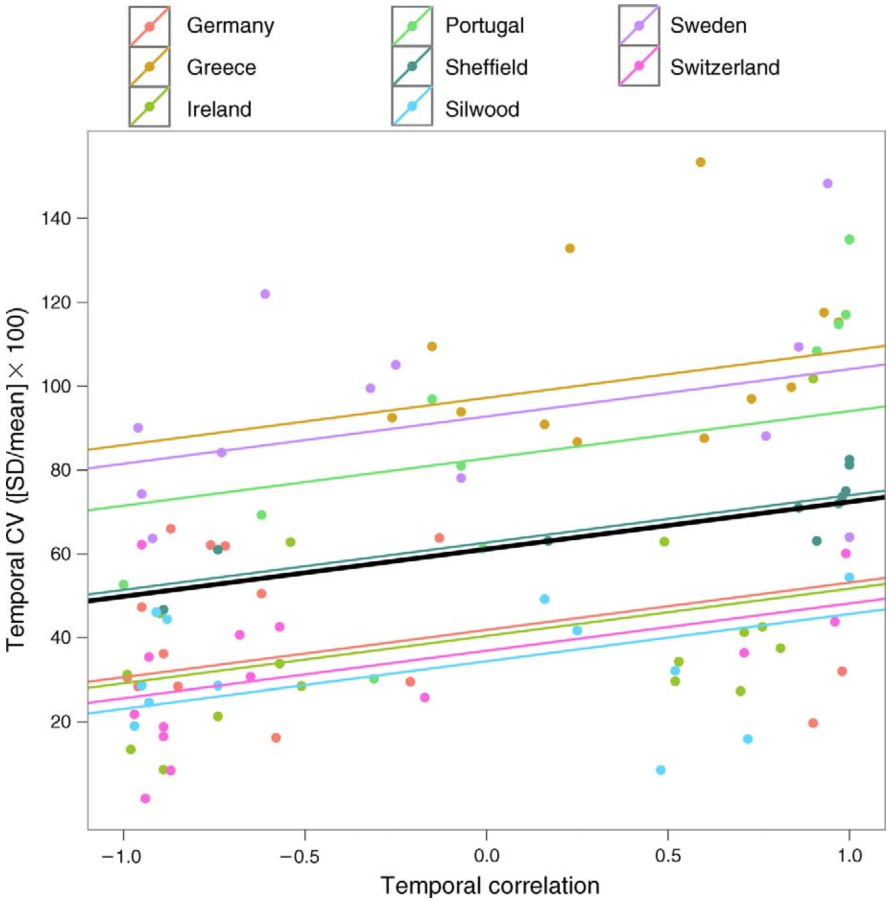

FIG. 3. Temporal variability (CV) of total community biomass of two-species mixtures as a function of the temporal correlation between the species in each pair. Negative correlations (standardized negative covariances) are associated with greater temporal stability (lower temporal CV) as predicted by the insurance hypothesis and related theory. The black line is the significantly positive linear regression slope (the fixed effect for the temporal correlation) from the mixed-effects model reported in the results, and the colored points and lines in the background indicate the variability in the relationship across sites (the random intercepts for the relationship at different sites).

(Loreau and de Mazancourt 2008). We can compare the relative effects of population asynchrony and overyielding, but only for this subset of the data. At this level of diversity population asynchrony is the dominant stabilizing effect (Fig. 3) since there is no significant effect of overyielding on temporal variability when restricted to the two-species mixtures (Appendix I). This weakening of the overyielding effect in two-species mixtures is consistent with the positive relationship between diversity and overyielding shown by previous analyses (Loreau and Hector 2001, Spehn et al. 2005).

Theory on stabilizing effects of the population fluctuations usually gives all species equal abundance as a simplifying assumption (but see Schwartz et al. 2000). However, potential stabilizing effects are strongly influenced by abundance since species that remain at relatively low biomass are limited in the contribution they can make to the aggregate community (Petchey et al. 2002). Unrealistic levels of evenness in experimental communities could therefore limit comparison with insurance effects in natural (non-experimental) communities. For five of our experiments we compared relative abundance distributions of the diverse experimental communities to matched "reference" plots in neighboring natural grasslands (see Hector et al. 2007) using Simpson's evenness index (Magurran 2003). A mixed-effects analysis with site as a random effect showed no significant difference in evenness between the most diverse experimental communities and the natural reference plots (difference in Simpson's index = −0.028; 95% CI = −0.116–0.060; Appendix J). Therefore, while our experimental communities started with even relative abundance distributions, patterns of dominance rapidly developed which were indistinguishable from those of the natural grasslands within three years.

In summary, our results support the predictions that diversity has a destabilizing effect on the temporal fluctuations of individual populations but a stabilizing effect on ecosystem net primary production. The stabilizing effect is generated by a combination of asynchronous population fluctuations and overyielding (an increase in the temporal mean relative to the standard deviation). Positive selection effects had no detectible stabilizing influence. Our current data and methods are not able to address what role competition plays in generating asynchrony relative to intrinsic differences in species responses to temporal variation. Our results confirm the predictions of the insurance hypothesis and, together with earlier studies, suggest that stabilizing effects of diversity on ecosystem productivity may be relatively widespread in plant communities.

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APPENDIX A

Spatial CVs (*Ecological Archives* E091-155-A1).

APPENDIX B

Summary of the analysis of the temporal CVs as a function of species richness and the organizational level (*Ecological Archives* E091-155-A2).

APPENDIX C

Temporal variability (CV) calculated after randomly assigning the two replicate plots of each mixture to either the population CV or the community CV omitting the functional group level (*Ecological Archives* E091-155-A3).

APPENDIX D

Temporal variability (CV) for individual sites (*Ecological Archives* E091-155-A4).

APPENDIX E

Pseudo R^2 for each site (*Ecological Archives* E091-155-A5).

APPENDIX F

Temporal mean and SD for individual sites (*Ecological Archives* E091-155-A6).

APPENDIX G

Mean–SD relationships for individual sites (*Ecological Archives* E091-155-A7).

APPENDIX H

Temporal CV as a function of the selection effect (*Ecological Archives* E091-155-A8).

APPENDIX I

Summary of the analysis of temporal CVs as a function of overyielding for the two-species mixtures only (*Ecological Archives* E091-155-A9).

APPENDIX J

Comparison of rank-abundance curves for experimental and reference plots (*Ecological Archives* E091-155-A10).

SUPPLEMENT

The data sets used in the paper with detailed descriptions (*Ecological Archives* E091-155-S1).