

Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities

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Abstract. The loss of biodiversity is thought to have adverse effects on multiple ecosystem functions, including the decline of community stability. Decreased diversity reduces the strength of the portfolio effect, a mechanism stabilizing community temporal fluctuations. Community stability is also expected to decrease with greater variability in individual species populations and with synchrony of their fluctuations. In semi-natural meadows, eutrophication is one of the most important drivers of diversity decline; it is expected to increase species fluctuations and synchrony among them, all effects leading to lower community stability. With a 16-year time series of biomass data from a temperate species-rich meadow with fertilization and removal of the dominant species, we assessed population biomass temporal (co)variation under different management types and competition intensity, and in relation to species functional traits and to species diversity. Whereas the effect of dominant removal was relatively small (with a tendency toward lower stability), fertilization markedly decreased community stability (i.e., increased coefficient of variation in the total biomass) and species diversity. On average, the fluctuations of individual populations were mutually independent, with a slight tendency toward synchrony in unfertilized plots, and a tendency toward compensatory dynamics in fertilized plots and no effects of removal. The marked decrease of synchrony with fertilization, contrary to the majority of the results reported previously, follows the predictions of increased compensatory dynamics with increased asymmetric competition for light in a more productive environment. Synchrony increased also with species functional similarity stressing the importance of shared ecological strategies in driving similar species responses to weather fluctuations. As expected, the decrease of temporal stability of total biomass was mainly related to the decrease of species richness, with its effect remaining significant also after accounting for fertilization. The weakening of the portfolio effect with species richness decline is a crucial driver of community destabilization. However, the positive effect of species richness on temporal stability of total biomass was not due to increased compensatory dynamics, since synchrony increased with species richness. This shows that the negative effect of eutrophication on community stability does not operate through increasing synchrony, but through the reduction of diversity.

Key words: *compensatory dynamics; dominant removal; fertilization; eutrophication; functional (dis)similarity; grassland; species richness; synchrony.*

INTRODUCTION

How biological diversity and ecosystem functions are maintained in time is one of the fundamental questions in ecology. Changes and fluctuations in the environment (including weather conditions) cause variation in different components of community structure and functioning. What determines the stability of communities under such fluctuations remains one of most debated questions in both theoretical and applied ecology (Pimm 1984, Isbell et al. 2015), with the idea that biodiversity begets stability being one of the long-lasting paradigms

(MacArthur 1955, Goodman 1975, Loreau and de Mazancourt 2013, Hautier et al. 2015). Nevertheless, other factors have been demonstrated to be at least as important for stability as diversity, particularly the characteristics of the environment, including management and productivity of the environment, and species life history strategies (Lepš et al. 1982, Lepš 2004, Májecková et al. 2014, Zhang et al. 2016b). Rapidly increasing rates of species extinction and ecosystem modification call for an urgent understanding of how ecosystem structure, functioning, and services will be altered following realistic biodiversity loss (Isbell et al. 2015).

There are several components of stability of ecological communities (Pimm 1984, Lepš 2013), a key one being *constancy*, usually characterized by its reciprocal *variability* over time (high variability means low constancy). In

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empirical studies of grasslands for example, the temporal variability of the total community biomass at the peak of the vegetation season (a surrogate for annual productivity), or of the biomass of individual species, are often used. The temporal variability of the biomass is usually measured as a coefficient of variation ($CV = \text{standard deviation}/\text{mean}$; both calculated over a time series of values). The variability of total community biomass is to some degree determined by the variability of biomass of individual populations; if the individual populations do not fluctuate, the total community biomass will not fluctuate either. On the contrary, even if individual populations undergo pronounced fluctuations, the total biomass can be rather stable (Tilman 1996). This can occur if fluctuations of individual species populations compensate each other, i.e., when the decrease of one or more species is compensated by an increase in other species. If coexisting species fluctuate completely independently of each other, and have the same mean and standard deviation in biomass (thus the same CV), then the CV of total biomass decreases with the square root of the number of species (the stabilizing effect of diversity or “portfolio effect”; Doak et al. 1998). In real communities, both the unequal representation of species typical of any ecological community (canonized by models of abundance distribution, e.g., Magurran 2004), and the tendency of less abundant species to fluctuate more than that of abundant species (Wolda et al. 1992, Lepš 1993, 2004, Bai et al. 2004) generally act to weaken the portfolio effect. The strength of the portfolio effect is further affected by the fact that species often do not fluctuate independently of each other (Houlahan et al. 2007, Valone and Barber 2008).

The degree of synchrony in fluctuations of individual species populations in a community is an important factor affecting the stability of communities (Hector et al. 2010, Bluthgen et al. 2016). If there is a perfect positive correlation between all species pairs (perfect synchrony), then the total biomass CV will be the same as the CV of individual species (the species are expected to have the same CV here), nullifying the portfolio effect; any positive correlation decreases the strength of the portfolio effect. The positive temporal correlation among species is generally attributed to the concordant species response to variation in environmental conditions. Very often, while most environmental conditions (e.g., soil nutrients) are rather stable, the main cause of species biomass variability is weather fluctuation across years. However, synchrony will never be perfect, because individual species will not respond in exactly the same way to environmental fluctuations and, particularly at smaller spatial scales, because of demographic stochasticity (de Mazancourt et al. 2013). Any deviation from perfect synchrony leads to some stabilization of community biomass. The negative temporal correlation among individual species is called compensatory dynamics (the decrease of biomass of one species is compensated by increase of another species) and further fosters the stabilization of total biomass. Compensatory dynamics are

generally attributed, particularly between plants, to the effect of interspecific competition (Tilman 1996); theoretically, they can be caused also by discordant or differently timed species response to weather fluctuations (Loreau and de Mazancourt 2013). Note, however, that the term “compensatory dynamics” is not used consistently by various authors, whereas Houlahan et al. (2007) considers compensatory dynamics as only the prevalence of negative temporal correlations (in their definition prevalence of negative covariances), other authors (e.g., Loreau and de Mazancourt 2013, Song and Yu 2015) have less strict definitions. The term “asynchrony” is used even more inconsistently. Here, we consider (partial) synchrony as the prevalence of positive correlations (or covariances), and compensatory dynamics as negative correlations (or covariances). We will refer to synchrony measures for the statistics characterizing the phenomenon of species covariation.

The analysis of available time series has shown that the prevalence of compensatory effects could be rather exceptional in biological communities (Houlahan et al. 2007, Valone and Barber 2008). Nevertheless various factors can contribute to a partial stabilization of communities. The prevailing environmental characteristics of a site, namely the environmental productivity, can affect the degree of species fluctuations and also the factors affecting the strength of the portfolio effect: species richness and the degree of synchrony. For example, the same species fluctuate more in fertile than in infertile conditions (Lepš 2004, Májeková et al. 2014). It is also well known that eutrophication is one of the most important drivers of diversity decline in seminatural meadows, and this fact has been repeatedly demonstrated experimentally (e.g., Hautier et al. 2014, Lepš 2014). Synchrony has also been shown to increase with eutrophication (Hautier et al. 2014, Song and Yu 2015, Zhang et al. 2016b), although the increase of asymmetric competition for light with increased productivity should actually cause increased compensatory dynamics. Similarly the decrease in biomass of one species (particularly the dominant) could allow other species, often subordinate ones, to increase their biomass, thus supporting compensatory effects. Indeed, we have demonstrated that dominant removal in a meadow community leads to an immediate increase in total biomass of the other species present (Lepš 1999). A possible trade-off between competitive strength and resistance to adverse weather (Grime and Pierce 2012) can lead to a negative temporal correlation of some pairs of species.

Loreau and de Mazancourt (2013) have argued that species diversity’s stabilizing effect should be strongest when communities, with compensatory dynamics, consist of species that respond differently to biotic and abiotic conditions (“insurance hypothesis”). It has been hypothesized that the differences in response will be connected to differences in functional traits connected to resource acquisition, thus more functionally distinct species will be less synchronous (Adler et al. 2013). This theoretical prediction has been tested, to the best of our knowledge, only

by Vergnon et al. (2009) using phytoplankton body mass. Unfortunately, no distinction between positive and negative correlation between species was assessed in that study, and such a distinction is essential to distinguish potential mechanisms behind community fluctuations. Roscher et al. (2011) demonstrated that, in the Jena experiment, the species within a priori defined functional groups have a tendency toward synchrony, whereas some compensatory dynamics were found between functional groups. Although no functional traits were directly considered in this test, the groups were delimited partially according to species traits, so species are more similar within groups than between groups.

It is known that species fluctuations depend on the traits of individual species, with species with traits corresponding to conservative strategies fluctuating less (Májeková et al. 2014). In unitary organisms, where the potential growth rate can be calculated on the basis of individual fecundities, species with high potential growth rate exhibit high temporal variability (Lepš et al. 1998). Accordingly prevailing species strategies and species traits can be good predictors of community stability (Lepš et al. 1982, Adler et al. 2006, Angert et al. 2009, Polley et al. 2013). We can speculate, on one hand, that negative correlations will occur more often for pairs of the most functionally dissimilar species, because similar species are more likely to respond to weather fluctuation in a harmonious manner. On the other hand, negative correlations can also occur in pairs of species similar in resource use traits because these will use resources in a similar way and thus will be in stronger competition.

In this context, using temperate grasslands as a study system, we aimed to assess patterns of species biomass temporal (co)variation under different management types and competition intensity, and to relate these patterns to species traits and to species diversity. In temperate grasslands, we can expect both the existence of interspecific competition and the concordant responses of most species to interannual weather fluctuations. It is, however, not clear which of these processes prevail under various management and competition intensity scenarios. We used 16 years of data on individual species biomass from a long-term field experiment with regular fertilization and dominant removal (removing its competitive effect) as the main treatments (Lepš 2014, Májeková et al. 2014). We asked (1) how the total community biomass and its variability, the variability of individual species biomass, the degree of synchrony in species fluctuation and species diversity are affected by fertilization and the presence of the dominant species; (2) whether partial synchronization or compensatory dynamics prevail in a species-rich seminatural community; and (3) if the covariation (temporal correlation) of pairs of species is affected by their mutual similarity in terms of their functional traits. Following these questions we attempted to determine the causal pathways of the effect of fertilization on the variability of total community biomass (i.e., on the characteristics usually employed to measure community stability).

METHODS

Study site and experimental design

The study site is located 10 km southeast of České Budějovice, Czech Republic (48°57' N, 14°36' E, altitude 510 m). During the experiment (between 1999 and 2014), the average annual precipitation was 721 mm (minimum 486.6 mm and maximum 1288.4 mm), and average annual temperature was 8.15°C (minimum 6.2°C and maximum 9.3°C; data for precipitation comes from the Ledenice meteorological station, ~4 km from the experimental site, data for temperature comes from a meteorological station in České Budějovice, corrected for the altitude difference). The plant community is an oligotrophic wet species-rich meadow (over 30 species of vascular plants per m²) dominated by a tussock grass, *Molinia caerulea*. Other more abundant species included mostly grasses and about 10 species of sedges (*Carex* spp.). The meadow, similar to those in the surrounding region, has traditionally been extensively mown for centuries.

In 1994, 12 permanent mown plots were established, each 2 × 2 m. Fertilization and dominant removal were applied as treatments in a factorial design. The four treatment combinations (fertilization and removal, fertilization and no removal, no fertilization and removal, no treatment) were repeated three times. In all the figures, Rem–, Rem+ means no removal and removal, respectively, Fert–, Fert+ means no fertilization and fertilization, respectively. The fertilization treatment consisted of annual application of 65 g/m² of a commercial NPK fertilizer (12% N as nitrate and ammonium, 19% P as P₂O₅, and 19% K as K₂O, corresponding to 7.8 g of N, 12.4 g of P, and 12.4 g of K per m²). Since 2003, the commercial fertilizer was changed to Cererit (8% N, 13% P, 11% K), and in 2012, the total dosage was reduced to 50 g/m² (corresponding to 4 g of N, 6.5 g of P, and 5.5 g of K per m²), in order to prevent the accumulation of nutrients, particularly phosphorus, in the soil. *Molinia caerulea* tillers were manually removed with a screwdriver in April 1995 with a minimum of soil disturbance and new individuals of *M. caerulea* were removed annually.

Species' biomass was recorded each year in the second half of June in the central 0.25 m² of each plot. Biomass was clipped to mimic mowing and was sorted into species, oven-dried, and weighed (technical details are presented in Appendix S1). The clipping was applied to the central part of the plot and the rest of the plot was mown as well. During the first five years (1994–1998), vegetation dynamics were largely governed by directional responses to the applied treatments (Lepš 1999), thus we omitted these years from our analyses, all the analyses are based on the data from 16 years, 1999–2014. Note that biomass was always taken from an identical, permanently marked area, and so the variation corresponds only to temporal variability and cannot be confounded by spatial variability. More details about the experimental setup are given in (Lepš 1999, 2004, 2014).

Diversity and variability measures

Species richness of each plot was expressed as the number of species recorded, at least once, in the biomass of the central 0.25-m² quadrat during the 16 years (1999–2014), as these are the species considered to participate in the functioning of the community. We also calculated the average species richness of a plot (average of species richness values over the 16 years).

Because it is expected that the portfolio effect will be strongest when all the species are equally represented, for each plot we have calculated also the effective number of species (ENS), as a reciprocal of Simpson index of dominance

$$\text{ENS} = \frac{1}{\sum_{i=1}^{\text{nsp}} p_i^2} \quad (1)$$

where p_i is the proportion of i th species in biomass (averaged over all the years) and nsp is total number of species in the community.

For each plot, we have calculated CV_{comm} , i.e., the coefficient of variation (standard deviation/mean) of the total community biomass, and CV for each species. CV is considered to be a reliable estimator of temporal variability (McArdle and Gaston 1995), and it is also the most widely used (sometimes in a squared form, or a reciprocal value as a measure of constancy). To characterize how much individual populations on average fluctuate within the community, we calculated the weighted average of CV of individual species (CV_{WA}). The weighting is necessary (see Bluethgen et al. [2016] for further justification), because very rare species often vary more than abundant species (for example, a species found just once with negligible biomass during the 16 years would have the maximum possible CV, for 16 years, this value is 4), and its effect on the total biomass is within the sampling error. The relative representation of the species during the whole 16 years was used as a weight. With this weighting, excluding the very rare species is not necessary, simply because their weight (and thus effect on the weighted average) is negligible.

Synchrony measures

Measuring synchrony in temporal fluctuation is not a trivial task. This is partially because of the asymmetry of positive and negative correlations, when we consider more than two variables, any number of variables can show absolute positive correlation (i.e., correlation coefficient $r = 1$ for each pair of variables), whereas if two variables are absolutely negatively correlated, i.e., their $r = -1$, any third variable will either be completely uncorrelated with both of them (i.e., $r = 0$), or will be positively correlated with one and negatively with the other. Hence the average pairwise correlation cannot be used for this purpose (see Gross et al. [2014] for further details).

A comparison with the null model of independent fluctuations of individual species is best achieved on the basis of basic probability rules (Lepš 2004): if the species fluctuate completely independently of each other, then the variance (here the variance over years) of community biomass equals the sum of variance of individual species, i.e.,

$$\text{var}\left(\sum_{i=1}^{\text{nsp}} x_i\right) = \sum_{i=1}^{\text{nsp}} \text{var}(x_i) \quad (2)$$

where x_i is biomass of the i th species and nsp is total number of species in the community, so that the left side of the equation is the variance of community biomass. If the community variance is higher than expected under the independence hypothesis, then the fluctuations are (at least partially) synchronized, smaller variance of the community suggests that there are some compensatory dynamics at play, i.e., the increase in one species is compensated by a decrease of other species. Note that if the real variance of the total is bigger than expected, then the sum of covariances is positive, if it is smaller, the sum of covariances is negative; so the comparison is equivalent to those of Houlahan et al. (2007). This suggests that a useful measure of synchronization could be expressed as the ratio of observed to expected variance (i.e., the ratio of variance of community biomass to sum of variances of biomass of all the species; see Roscher et al. 2011, Cadotte et al. 2012, Hallett et al. 2014). Because this value will be highly positively skewed, we used a log-transformation (decadic log in our case), which results in values centered around zero in the case of independent fluctuation. We call this the “log var ratio”

$$\log \text{var ratio} = \log\left(\frac{\text{var}\left(\sum_{i=1}^{\text{nsp}} x_i\right)}{\sum_{i=1}^{\text{nsp}} \text{var}(x_i)}\right) \quad (3)$$

where x_i is biomass of the i th species and nsp is total number of species in the community.

Positive values of log var ratio signify (partial) synchronization, negative values indicate compensatory dynamics. The advantage of this measure is that it is positive if the total biomass fluctuates more than it would under the assumption of species independence and negative in the opposite case. The disadvantage is that the lower limit would be minus infinity (in the case of perfect compensation, where the total biomass is totally constant), and the upper limit is given by the number of species and their equitability. Note, that in this measure, the effects of individual species will be generally proportional to their variances, which is usually scaled by the mean. Consequently, the effect of rare species will be negligible.

Recently, Gross et al. (2014) suggested a new measure of synchrony η , and Bluethgen et al. (2016) used its weighted form. Results of their use are very similar to the use of the log var ratio, and we thus present them only in Appendix S2.

To relate individual variability and synchrony measures to the experimental treatments, and to species richness, standard methods of ANOVA, regression, and general linear models were used.

Plant functional traits

In 2013 we measured, directly in experiment plots, the following set of functional traits: plant height, leaf dry matter content (LDMC), specific leaf area (SLA), leaf N, leaf C, leaf $\delta^{13}\text{C}$, and leaf $\delta^{15}\text{N}$. We measured all traits values following Pérez-Harguindeguy et al. (2013) for a minimum of five individuals in each treatment combination. SLA represents the ratio of leaf area to dry mass (m^2/kg), while LDMC represents leaf dry mass divided by the fresh mass (mg/g). Leaf N concentration is the total amount of N per unit of dry leaf mass (mg/g). Across species, it tends to be closely correlated with mass-based maximum photosynthetic rate and with SLA (Pérez-Harguindeguy et al. 2013). Leaf C concentration represents the total amount of C per unit dry leaf mass (mg/g). Leaf $\delta^{13}\text{C}$, which measures the ratio of ^{13}C over ^{12}C (‰), is an integrated, long-term measure of the ratio between internal and ambient CO_2 concentrations (C_i/C_a) that reflects the intrinsic water use efficiency of plants (Farquhar et al. 1982). Leaf $\delta^{15}\text{N}$ has been employed as an indicator of responsiveness to nitrogen acquisition (Robinson 2001).

We analyzed whether species temporal correlations were related to differences in functional traits between species. The analyses were carried out on the most frequent species that were present in at least five years and had an average biomass higher than 0.02 g. The selection criteria yielded 36, 33, 51, and 48 species in the treatment combination of fertilization and removal, fertilization and no removal, no fertilization and removal, and no treatment, respectively. To compute species pairwise temporal correlations, we pooled species' biomass of the three replicated plots per treatment combination. Subsequently, we computed Pearson's correlation coefficient of species biomass in time (16 years) between each pair of species and created a correlation matrix for each treatment combination.

For all traits combined we computed a dissimilarity matrix using the Euclidean distance (R software, R Development Core Team 2016) with traits standardized to the z-score (Laliberté and Legendre 2010). We then tested the relationship between the correlation matrix and the trait dissimilarity matrix in each treatment combination with the Mantel test using package *vegan* (Oksanen et al. 2015). The probability is determined by permutations (999 permutations for each test). As we considered both alternative hypotheses (i.e., both positive and negative correlation), and thus used the two-sided test, we report $2 \times$ one-sided P (i.e., two times the probability of r being more extreme than expected by chance) as the P value in the results. Because we got significant results using the combination of all traits together, we then

aimed to reveal which traits are responsible for the relationship, and thus applied similar procedure for each trait separately.

RESULTS

Response of community parameters to the experimental manipulations

As expected, mean biomass increased with fertilization, and we found no effect of *Molinia* removal on the total biomass at all (Table 1, Fig. 1a). This shows that the removed *Molinia* biomass was fully offset by other species, and thus confirms the existence of strong competition within the community. The number of species (i.e., all the species detected at least once during all the 16 years in the plot) decreased with fertilization, while removal had no effect at all (Table 1, Fig. 1b). As this cumulative number of species found in a plot was highly correlated with the average number of species in a plot ($r = 0.95$ for the 12 plots) both sets of results were nearly identical for the two variables, and only the cumulative number of species is presented as species richness further on. Note the very high number of species detected in the plots of 0.25 m^2 . This is the effect of species turnover, i.e., several species are found in a plot for few years only. Nevertheless, the average numbers of species are also rather high for the unfertilized plots (average 34.4 per 0.25 m^2), and not very low for the fertilized plots (19.1 per 0.25 m^2).

The effective number of species was negatively affected by fertilization and positively affected by dominant removal, and there was also a highly significant interaction: the effect of removal was much more pronounced in unfertilized plots (Table 1). Thus, although the dominant removal did not increase the total number of species, it increased the effective number of species, through decreasing the dominance of a single species. This means

TABLE 1. Results of two-way ANOVAs (factors fertilization and dominant removal) for characteristics of biomass, species richness, and biomass variability.

Response	Fertilization		Removal		Interaction	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Average total biomass	42.43	<0.001	0.24	0.635	1.64	0.235
Number of species	36.00	<0.001	0.30	0.600	0.13	0.726
Effective number of species	31.69	<0.001	36.77	<0.001	11.97	0.009
CV_{comm}	10.34	0.012	3.58	0.095	0.01	0.925
CV_{WA}	2.27	0.170	12.47	0.008	0.01	0.911
log var ratio	6.46	0.035	0.12	0.735	0.09	0.776

Notes: The test criterion F (in all cases $\text{df} = 1, 8$) and corresponding probability P is presented for the main effects and their interaction. CV_{comm} , coefficient of variation of total biomass; CV_{WA} , weighted average of individual species coefficients of variation.

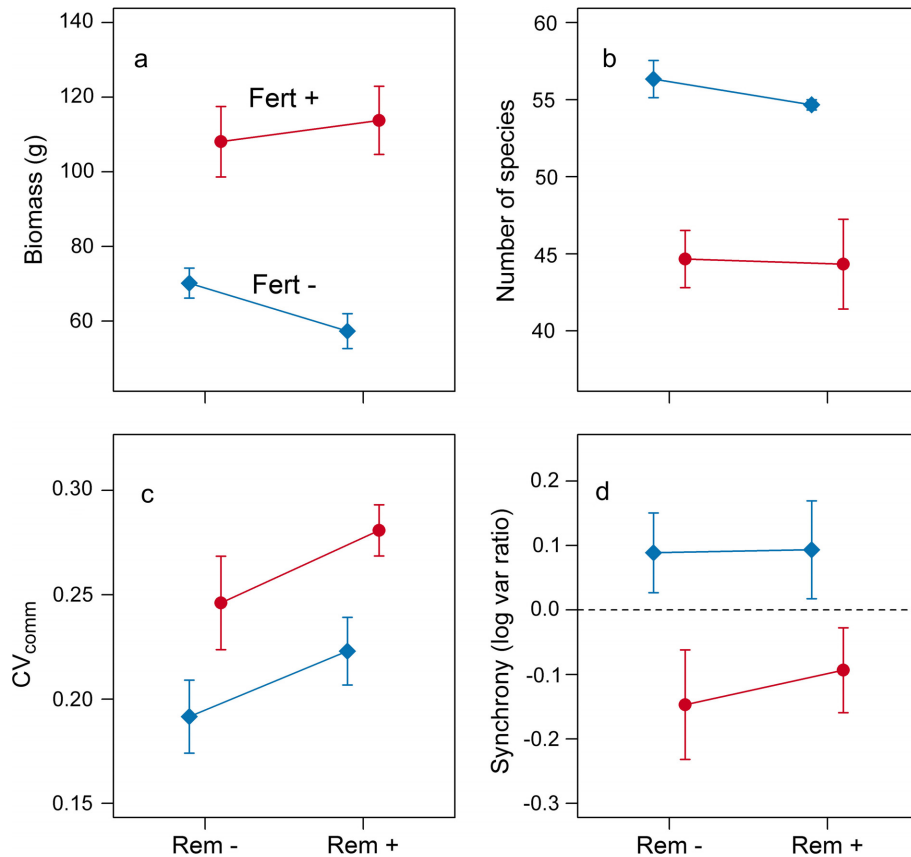


FIG. 1. The response of (a) average biomass recorded in 0.25 m², (b) number of species, (c) CV of total biomass (CV_{comm}), and (d) synchrony measured as the log var ratio to fertilization (Fert +, fertilized; Fert -, not fertilized) and dominant removal (Rem +, dominant removed; REM -, dominant not removed). The bars are standard errors. The lines are added to better visualize the interaction (parallel lines indicate no interaction). The results of two-way ANOVAs for all the characteristics are presented in Table 1.

that the removed biomass of *Molinia* was replaced by multiple other species.

The variability of the total community biomass CV_{comm} was significantly higher in the fertilized plots (Table 1, Fig. 1c). We also detected higher CV_{comm} values in the removal plots (concordantly in the fertilized and unfertilized plot), but this effect was only marginally significant ($P = 0.095$, Table 1). The average variability of individual species (CV_{WA}) was significantly positively affected by dominant removal, and non-significantly increased by fertilization (Table 1). Note that this does not necessarily mean that the species fluctuate more in the removal plots, as this may result from the fact that *Molinia* was one of the most stable species in the community and, because of its high proportion, its presence decreased the weighted average.

Synchrony

Fertilization significantly decreased synchrony (log var ratio), whereas the dominant removal had no effect on synchrony, neither itself, nor in the interaction with

fertilization (Table 1, Fig. 1d). Moreover, the results suggest that in the unfertilized plots, some synchronization prevails, whereas in the fertilized plots, we see some tendency toward compensatory dynamics. The grand mean over all the plots was very close to zero (mean = -0.015 , SE = 0.048). The results for other synchrony measures were similar to the log var ratio (Appendix S2: Table S1, Fig. S1).

Relationships among community parameters

The variability of total biomass (CV_{comm}) decreased with species richness ($R^2 = 0.666$, $P = 0.001$, Fig. 2a). This decrease was largely driven by the fertilization treatment, with species-rich and more constant unfertilized plots on one hand, and species poor and more variable fertilized plots on the other. Nevertheless, the stabilizing effect of species richness remained significant even after accounting first for the effect of fertilization (in the sequential, i.e., Type I sum of squares GLM, $F_{1,9} = 5.83$, $P = 0.038$); if the effect of species richness was fitted first, the effect of fertilization was not

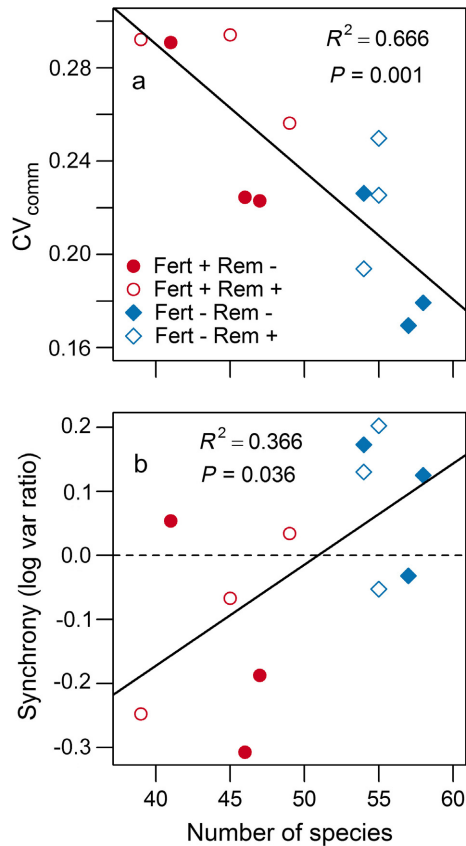


FIG. 2. Relationship between (a) number of species and coefficient of variation of the whole community (CV_{comm}) and (b) number of species and species synchrony measured as the log var ratio. Applied treatments were fertilization (Fert+ [Fert- means no fertilization]) and dominant removal (Rem+ [Rem- means no removal]).

significant. The variability of individual species CV_{WA} was marginally significantly correlated with CV_{comm} ($r = 0.539$, $P = 0.070$), and non-significantly decreased with the number of species ($r = -0.48$, $P = 0.114$).

There was a very tight negative correlation of the average biomass with number of species ($r = -0.903$), and less pronounced negative correlation with the effective number of species ($r = -0.667$), both highly significant. CV_{comm} was also positively correlated with the total biomass, but this effect disappeared after accounting first for the fertilization effect. Nevertheless, because the average total biomass is in the denominator of CV_{comm} , this shows that the temporal variability (expressed as standard deviation) is increased by fertilization more than the total biomass.

Synchrony (log var ratio) increased with species richness ($R^2 = 0.366$, $P = 0.036$, Fig. 2b). Moreover, contrary to expectation, CV_{comm} was generally uncorrelated with the synchrony (for log var ratio, the correlation is even non significantly negative, $r = -0.219$). We found no significant relationship between any measure of

biomass variability or synchrony, and the effective number of species.

The total variability of biomass CV_{comm} should be a result of variability of individual species (the higher variability of individual species, the higher variability of total biomass), of synchronization of individual species (the higher synchrony, the higher CV of total biomass), and of the number of species present (the more species, the stronger the portfolio effect). The (Type III sum of squares) multiple regression of CV_{comm} on these three characteristics showed a significant effect of all of these variables in the expected directions, with the effect of the number of species being by far the most pronounced. The standardized partial regression coefficients were -0.99 , $+0.56$, and $+0.36$ for number of species, log var ratio and CV_{WA} , respectively. Interestingly, although the plain correlation of CV_{comm} and log var ratio was (non-significantly) negative, after accounting for the effect of species richness (which was highly positively correlated with log var ratio; Fig. 2b), the effect of log var ratio was significantly positive, and the effect of CV_{WA} was also significantly positive.

Plant functional traits

We found significant negative relationships between the pairwise species temporal correlations and their functional traits dissimilarity based on all the measured traits together (Fig. 3). The significant negative relationship was found in all the treatment combinations (fertilization and removal $r = -0.18$ and $P = 0.028$, fertilization and no removal $r = -0.18$ and $P = 0.036$,

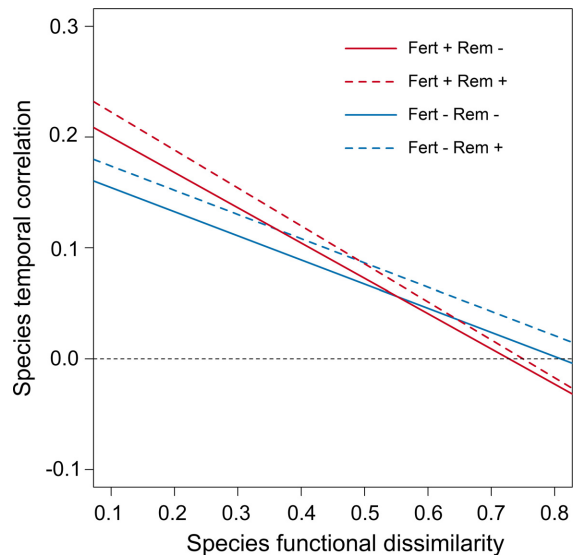


FIG. 3. Negative relationship between species temporal correlation and species functional dissimilarity (based on multi-trait approach) for all four treatment combinations. Applied treatments were fertilization (Fert+ [Fert- means no fertilization]) and dominant removal (Rem+ [Rem- means no removal]).

no fertilization and removal $r = -0.11$ and $P = 0.010$, and no treatment $r = -0.11$ and $P = 0.016$). However, when examining single traits the relationships were generally weaker and less consistent (Appendix S3: Table S1), and the number of significant relationships only slightly exceeded that expected as a result of Type I error rate. Nevertheless, all the significant and marginally significant relationships were negative, although it is clear that there is no single trait that, alone, would be responsible for the negative correlation pattern observed when combining all traits together.

DISCUSSION

Species fluctuations in species-rich communities were mostly independent of each other, although the extent of fluctuations and synchrony depended upon management and species' functional traits. We detected a slight prevalence of synchrony in unfertilized conditions and a tendency toward compensatory dynamics in fertilized conditions, which are contrary to the majority of the results reported previously. The general independence of individual species fluctuations, one of the assumptions by Doak et al. (1998) to demonstrate "the statistical inevitability of stability–diversity relationships" (the portfolio effect) is not substantially violated in our data; the small violation of the independence assumption should (slightly) enforce and suppress the portfolio effect in fertilized and unfertilized conditions, respectively.

Effects of experimental manipulations: possible causal pathways

The removal of the dominant species significantly increased the effective number of species (ENS), the average species fluctuation, and non-significantly increased the total biomass variability. Its effect on species richness, total biomass, and synchrony was negligible. The increase of ENS is not surprising, when the dominant species is removed then the equitability increases, and this leads necessarily to the increase of ENS. Nevertheless, it shows that none of the species was able to entirely replace the removed dominant. The lack of effects on the number of species also shows that the increased space does not help other species to establish. *Molinia* is one of the most stable species in the plots (in non-removal plots, its CV is 0.37 as compared to the weighted average of all the species, which is 0.70). Its removal, thus, leads to considerable increase of the CV_{WA} , because the CV of other species is not changed by removal (Májeková et al. 2014). We were not able to fully demonstrate the significant destabilizing effect on the total biomass (nevertheless, the evidence is suggestive, $0.05 < P < 0.1$), probably because of relatively low number of replications resulting in the weak test (the replications are strongly limited by the dedicated and time-consuming biomass sorting in these species rich plots; see Appendix S1). The suggested stabilizing effect

of *Molinia* would confirm the importance of strong stable dominant for community stability (Valone and Balaban-Feld 2017).

The fertilization had multiple effects, implying that the eutrophication can have fundamental effects on grassland ecosystems. It increased the total biomass and also its fluctuation, decreased the number and the effective number of species, and led to the decreased synchrony with some tendency toward compensatory dynamics. It had only a non-significant (but positive) effect on the average fluctuation of individual species within communities. Whereas the destabilizing effect of fertilization on the total community biomass is unequivocal (as it is the experimental manipulation), the causal pathways need to be carefully taken into account, because the fertilization simultaneously affects several parameters of the community and therefore they must be inferred from correlations. The theory predicts that the community biomass variation (CV_{comm}) should decrease with species richness and with community equitability (Doak et al. 1998), and should increase with synchrony (Valone and Barber 2008), and with the variability of individual species (Doak et al. 1998). Some authors (Hector et al. 2010) expect that the variation could decrease with the productivity (i.e., with the average community biomass over the years), because this value is in the denominator of CV_{comm} (stabilizing effect of overyielding). Nevertheless, the CV_{comm} was higher in more productive fertilized plots, and these were less species rich than the unfertilized plots, so this stabilizing effect of diversity through overyielding, found in biodiversity experiments (Hector et al. 2010) cannot play a role in our data.

The negative correlation between the CV_{comm} and species richness was rather strong in our data, supporting the hypothesis of a stabilizing effect of species diversity. Indeed, the explanatory power of species richness was stronger than the explanatory power of fertilization, and remained significant even after accounting for fertilization first in the model. This corresponds well to the results of experiments with diversity experimentally manipulated (Roscher et al. 2011). Also, Isbell et al. (2015) showed that higher species richness caused higher resistance to climatic events; higher resistance should naturally lead to decreased variability. The higher explanatory power of species richness, even after accounting for the effect of fertilization, is important because in our experimental setup the changes in species diversity are not independent of fertilization. Indeed such a setup with independent diversity and fertilization treatments could be created artificially but it would not be naturally occurring in real meadows, and moreover artificially created assemblages often fail to establish the high species diversity communities (with species richness corresponding to our plots). As such, the results show that while fertilization can decrease synchrony it destabilized community biomass because the effect of species diversity was stronger.

We have then good reasons to believe that a relatively large proportion of the destabilizing effect of fertilization acts through the decrease in species richness and subsequent decrease of the portfolio effect. First, the increase of average fluctuation of individual species CV_{WA} with fertilization was only mild, whereas its effect on CV of the total biomass and also on the species richness was much more pronounced. Accordingly, the effects of CV_{WA} became significant only after accounting for the species richness (similar to the effect of synchrony). The individual populations were also destabilized by fertilization (Májeková et al. 2014), but this effect was not sufficient to explain the destabilization of the total biomass. However, this effect might be more pronounced in communities differing in their dominant species (e.g., Hallett et al. 2014, Zhang et al. 2016a). At the same time, fertilization decreased the synchrony (to the level of compensatory dynamics), so that in this way it should stabilize, rather than destabilize the total biomass. Then, the most plausible explanation for the destabilizing effect of fertilization is the decrease in the portfolio effect through the suppression of species richness. This conclusion is further supported by comparison with Hallett et al. (2014), where the species richness was a strong determinant of community stability, although some other relationship in their data were rather different from ours; in particular, in their case, the species number increased with annual precipitation (and thus also with the productivity, whereas in our data set, the opposite is true). In the experiments with manipulated diversity, the total biomass is positively related to species richness, however in our experiment, the relationship is negative; yet still, in both cases the total biomass variability decreases with species richness (Roscher et al. 2011, Venail et al. 2015).

Differences in species diversity in our plots were not directly manipulated, but resulted from the differences in management, mainly through fertilization. The diversity effects are thus necessarily confounded with the effect of fertilization. However, the advantage of our experimental setup is the natural species composition: the composition of unfertilized plots is typical for semi-natural extensive meadows (Lepš 2014), and the decline in species richness in fertilized plots mimics the species loss in real nature. Our results are thus relevant for species diversities that are also of conservationist's interest in real ecosystems. Indeed, our plots qualified for the richness records of the Czech Republic (Chytrý et al. 2015), and the number of species found over the time in 0.25 m² corresponds roughly to the highest sown species richness in the Jena experiment on 20 × 20 m (i.e., 1,600 times larger) plots, and the average species richness is several times higher than those from slightly larger plots in Tilman (1996), and also higher than the maximum species richness per 1 m² in Hallett et al. (2014).

Interestingly, the explanatory power of the effective number of species (ENS, which takes into account the number of species and equitability of species representation) was generally low (for both total variability and for

synchrony). This is probably because ENS is generally the only response variable that was strongly affected by dominant removal. The dominant species, *Molinia caerulea*, is a rather exceptional species in several functional characteristics (Lepš 1999, 2004), and fluctuates less than the other species. As it is the dominant, its removal increased the ENS, and, at the same time, the relatively constant part of the community was removed. Consequently, we did not observe the stabilizing effect of increased ENS.

Earlier we demonstrated that the same species fluctuate more in fertile conditions, and that species traits (namely the leaf dry matter content) are good predictors of the size of population fluctuations (Májeková et al. 2014). Accordingly, the weighted average of population fluctuations was higher in fertilized plots. Whereas the effects in Májeková et al. (2014) were significant, our results were not ($P = 0.17$). This is because, in the study from 2014, the basic unit of the statistical analysis was variability of individual populations (providing sufficient degrees of freedom to achieve high test power), whereas here we compare averages for individual plots with much lower df, and thus also a lower power of the test. Nevertheless, both analyses showed concordantly that the individual species fluctuate more in the less species-rich fertilized plots, which contradicts the predictions of Tilman (1996), who predicted increased fluctuations of individual populations in species-rich communities. Nevertheless, in our case, the change in CV_{WA} has probably no causal connection with species richness, but rather with the change from nutrient limitation in unfertilized plots (which is rather constant over years) to limitation by weather conditions in individual years (Lepš 2004).

Synchrony and competition

Fertilization decreased the synchrony to negative values, i.e., the fluctuations exhibited some compensatory dynamics, which is opposite to the results of Zhang et al. (2016b), Hautier et al. (2014), and Song and Yu (2015). The discrepancy might be due to the extent of the temporal scale considered, due to different nature of the studied systems, but also in the use of various measures of synchrony. All of the above papers use ϕ as a measure of synchrony (Loreau and de Mazancourt 2008), which is scaled between 0 for perfect compensation and 1 for perfect synchrony. We have not used this because, unlike Gross indices and log variance ratio, its value indicates decreasing synchrony (increasing asynchrony in their terminology) with the number of species, even where species fluctuate completely independently of each other (Thibaut and Connolly 2013, Gross et al. 2014). The value also does not indicate whether positive or negative correlations prevail (i.e., no comparison with the null model of independent fluctuation is possible). As a matter of fact, the mathematical relationship between ϕ and richness can be rather strong. In the simplest case, when all the species fluctuate completely independently, have

the same biomass, and also the same extent of fluctuations (the same simplifying assumptions as used by Doak et al. 1998), then we get $\phi = 1/n$, n being the number of species (Appendix S2). It is thus possible that the reported effects of decreasing synchrony (measured by ϕ) with fertilization are partially caused by a negative effect of fertilization on the species richness. Generally, if the synchrony is measured by ϕ , it is usually highly negatively correlated with (affected by) the number of species present (see the four data sets analyzed in de Mazancourt et al. [2013]). From this point of view, our results are quite in agreement with Roscher et al. (2011). In their case, the synchrony measured by ϕ strongly decreases with species richness, but the overall variance ratio is close to one and increases slightly with species richness (see Fig. 4a in Roscher et al. [2011]; note that their initial decrease is consequence of, by definition, the variance ratio for monoculture being 1). Our data provide similar pattern (Appendix S2).

The decrease in synchrony in our data is probably caused by increased competition for light in fertilized plots (Hautier et al. 2009). Kelemen et al. (2015) demonstrated that in our plots, competition, mainly the competition for light, increases with fertilization (in particular, the small plants are more suppressed by the surrounding vegetation). This is in perfect agreement with the arguments of Tilman (1996) predicting compensatory dynamics due to competition: in the asymmetric competition for light, the stronger competitors suppress the less competitive species under favorable conditions, which leads to compensatory dynamics. The fact that the dominant removal has no significant effect on the average community biomass also indicates strong competition. At the beginning of our experiment, we removed the dominant at the end of the vegetation season. The biomass of the rest of the community increased greatly in the next season (Lepš 1999), highlighting how strong competition can contribute to the stabilization of the community in the event of the loss of a dominant.

Synchrony and traits

Compensatory dynamics can arise from two mechanisms. The first one is the discordant reaction of the species to the environmental fluctuations and the second is competition. Similarly to the results of Roscher et al. (2011) and to the theoretical predictions by Adler et al. (2013) we found that the species synchrony was higher for functionally similar species. However, the pattern only arises when all traits are considered together; there is no single trait that would be able to consistently show this pattern. This suggests that the effect of functional similarity on similar responses to weather fluctuation is stronger than the possible increase in competition strength with increasing functional similarity. However, on the basis of the data we have, we are not able to fully separate these two mechanisms: this is simply because we see only the year-to-year ecological response of each

species (as it is affected by both weather fluctuation and competition), but not the physiological response (the distinction is exactly the same, as shown many years ago by Ellenberg [1953]) between ecological and physiological optima of species, see also Austin [1980]). We can hardly expect that the physiological response alone would be sufficient to create the compensatory dynamics as most species should benefit from optimal growing conditions, like warm and sufficiently wet springs. If some species within a community respond negatively to such favorable conditions, then it is simply because their physiological response is not as pronounced as for other species, and thus the competition equilibria shifted in favor of their competitors. For real separation of the physiological and ecological response, we would need to separate monospecific growths of individual species. As a matter of fact, the rest of the community (without *Molinia caerulea*) fluctuated roughly similarly when *Molinia* was present and in the removal plots (data not shown), but this can include also many interspecific relationship effects within the rest of the community.

Comparing our results with previously published analyses, it is clear that there is no single causal pathway, but that several factors affect the community biomass stability. The species richness conditioning the portfolio effect is of primary importance in the majority of cases (including our study). The importance of other factors, mainly the degree of synchrony and variability of the dominant species, varies with different environmental conditions.

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