

RESEARCH ARTICLE

Competition among functional groups increases asynchrony of their temporal fluctuations in a temperate grassland

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Abstract

Questions: We asked whether the competition among community components (a) destabilizes individual components; (b) increases the asynchrony of their fluctuations; and (c) stabilizes the total community biomass.

Location: Seminatural meadow in South Bohemia, Czech Republic.

Methods: We used biomass fluctuation data from a 13-year removal experiment. The plots used for this study contained, following experimental removal of other species, either mycorrhizal grasses only, mycorrhizal forbs only, or their mixture (grass “monocultures”, forb “monocultures”, and mixtures, respectively). Yearly peak aboveground biomass was available from ten blocks; biomass of the mixture plots was sorted into forbs and grasses. Temporal variability was characterized by coefficient of variation (CV) and synchrony by correlation coefficient, both calculated from the time series data.

Results: The variability of grass monocultures was higher than the variability of forb monocultures, which was slightly lower than the variability of mixtures. The variability of both grasses and forbs was higher in the mixture, where they are in competition with the other group, than in each of their respective monocultures. The correlation coefficients between the biomass of grass and forb monocultures within blocks were mostly positive, indicating that both groups tend to have similar physiological responses to weather fluctuations. The average correlation coefficient between the forbs and grasses in the mixture plots was significantly negative, thus reflecting the effect of competition between these two community components. The CV of the sum of forb and grass monocultures was similar to the CV of mixture plots.

Conclusions: Only competition between grasses and forbs leads to their negative mutual correlation, i.e., to compensatory dynamics. Our results support the hypothesis that competition has a destabilizing effect on individual community components (functional groups in our case) and increases asynchrony of their fluctuations. We have not found its stabilizing effect on the total biomass.

KEYWORDS

asynchrony, biomass fluctuation, compensatory dynamics, competition, functional groups, removal experiment, stability

1 | INTRODUCTION

The idea that diversity begets stability has a long tradition (MacArthur, 1955) and is partly based on the expectation that in diverse communities the decrease in abundance of one species can be compensated by increases in other species. The global decline in diversity has led to a new wave of interest in the effects of diversity on ecosystem functioning, including the effects on ecosystem stability. The experiments used to study the effects of diversity on stability are mostly based on sown mixtures (e.g., the Jena experiment, Roscher et al., 2011), where the species composition might still be quite different from a naturally developed species composition of real communities. Moreover, short-term experiments are often governed by directional changes (Lepš, 1999), and thus are not suitable for the evaluation of stability. The best chance to observe an effect of decreased diversity may perhaps lie in long-term removal experiments (Diaz, Symstad, Chapin, Wardle, & Huenneke, 2003). However, removal experiments in (semi)natural communities, lasting the numerous seasons needed to evaluate community stability, are rather scarce.

There are several components characterizing stability; the most commonly used are resistance, resilience, and constancy (Harrison, 1979). Constancy is an inverse of temporal variability, and thus constancy is sometimes called invariability (Wang et al., 2017). Variability is usually characterized by a coefficient of variation (CV, Doak et al., 1998), i.e., standard deviation divided by mean, both calculated from a temporal series. Doak et al. (1998) also demonstrated that unless the biomass values of the component species are perfectly positively correlated, the CV of the total biomass should decrease with the number of species. This effect is enforced if the individual species biomass values are negatively correlated over time, and the effect weakens if the variation of components is positively correlated (i.e., synchronized). Henceforth, we will concentrate on constancy, characterized by the variability of biomass through time and on the effect of (a)synchrony, an important determinant of total biomass variability of the community (Hautier et al., 2014; Song & Yu, 2015).

Low variability in total community biomass does not necessarily also mean low variability of biomass of individual populations (Tilman, 1996, 1999). The stabilizing effect of diversity is generally based on the concept of (at least partial) independence of temporal fluctuations of individual components (Doak et al., 1998) and on the concept of compensatory dynamics. Compensatory dynamics results from the situation when the decrease in biomass of one species in a community also implies a decrease in competition for the other species. As a result, the species released from competition might potentially increase their own biomass and in this way stabilize the total community biomass. Should competition be the main mechanism determining the fluctuations of species within a community, we would expect negative correlations between the biomass of different community components. On the contrary, Loreau and de Mazancourt (2013) stressed the importance of differential response of species to the fluctuating environmental conditions. Moreover, competition should have a destabilizing effect on individual populations (Loreau

& de Mazancourt, 2013; Tilman, 1996). As competition should destabilize individual populations, but might decrease the synchrony of their fluctuations, the resulting effect on the stability of total biomass depends on the magnitude of these two effects. As a matter of fact, depending on the model used, the theory predicts that competition should not stabilize communities (Ives, Gross, & Klug, 1999), or rarely, and that it would rather destabilize them (Loreau & de Mazancourt, 2013).

Inter-annual biomass variation in grasslands is probably affected mostly by the weather in individual years, because we can expect that the other environmental conditions do not change among years as much as weather does. As a result of this, we can expect some synchrony, i.e., positive correlation of individual species; for example, warm and wet spring is favorable for most species in temperate grasslands. But synchronization due to weather will be far from perfect — besides various stochastic factors, synchronization is limited by interspecific competition as described above, and the physiological responses of individual species might also differ considerably (physiological and ecological responses of species to weather conditions in individual years differ similarly to responses to any other environmental driver, as shown e.g., by Austin & Smith, 1989; Ellenberg, 1988). Even if we expect that most of the species will suffer from similar weather conditions, some species might be, e.g., more sensitive to a late spring frost (Inouye, 2008), whereas others might be sensitive to drought early in the vegetation season (Lepš, Osbornová-Kosinová, & Rejmánek, 1982). The strength of the response, its timing, or the climatic cue will very probably differ among individual species, as the sensitivity of individual species is closely connected with those species' life history strategies (Lepš et al., 1982; MacGillivray & Grime, 1995; Májková, de Bello, Doležal, & Lepš, 2014). Plant ecologists often think in terms of "horizontal communities" (Vellend, 2016), i.e., communities on the same trophic level, but synchrony might also be affected by higher trophic levels — weather favorable for plants might also be favorable for their pathogens or herbivores (which might, but need not, be species-specific), and differential sensitivity of plant hosts might also contribute to the observed asynchrony.

Whereas it is clear that the synchrony of population fluctuations will never be perfect, the published data and meta-analyses (Houlahan et al., 2007) show that in real communities partial synchrony prevails, but we can also find compensatory dynamics (i.e., the prevalence of negative temporal correlations), and in some cases, the fluctuations are on average close to the independence of individual species (neither positive, nor negative correlations prevail, also in our study Lepš, Májková, Vítová, Doležal, & de Bello, 2018). All the observed patterns result from counteracting processes — partial synchronization by weather and competition effects leading to compensatory dynamics or to a decrease of synchronization by weather. However, from the observed patterns, it is very difficult to deduce the processes. To demonstrate the effect of competition, we need to know the variability of individual components, growing without competition from the other components and thereby characterizing their physiological response, and their variability in



the whole community. Such data cannot be obtained from intact communities; we need manipulative experiments. Two possible kinds of experimental approaches include the sowing experiments of the Biodiversity–Ecosystem function (BEF) kind, like the Jena experiment (Roscher et al., 2011), and removal experiments. Based on the assumptions described in the preceding paragraphs, theory (Tilman, 1996) predicts that the total community biomass will fluctuate in time less than the biomass of monocultures of its components. On the contrary, the temporal fluctuations of individual species (or their groups) within communities should be higher (because they are enforced by competition) than the fluctuation of the same species (group) when grown in monocultures. Both these assumptions were confirmed by analyses of extensive data sets from various BEF experiments by Gross et al. (2014), who also demonstrated that the fluctuations of populations in communities are more asynchronous than fluctuations of their respective monocultures (in other words, the fluctuations governed by ecological responses of populations are more asynchronous than those governed by the physiological responses).

In the above paragraphs, we considered behavior of individual species – the species physiological response derived from the respective species monoculture is thus not affected by interspecific competition; however, within each species, intraspecific competition among individuals is still present. The ecological response is then composed of the physiological response, modified by competition of other species in the community. Similar reasoning can be applied if the considered community components are not individual species, but individual functional groups. The physiological response of the group then includes also the effect of competition within the functional group (both intraspecific, and between species of the same functional group), and the ecological response is modified by competition of other functional groups. In grasslands, grasses versus forbs are the most often used functional groups (Roscher et al., 2011), differing in many of their functional traits.

Long-term data series from natural communities, which enable us to test the above assumptions, are rather scarce. Here, we used data from a long-term removal experiment in a seminatural meadow. The term seminatural meadow is used for grassland communities where the species composition developed under long-term traditional management, typically regular mowing, which might last for decades or centuries. In this experiment (Šmilauer & Šmilauerová, 2013; Šmilauerová & Šmilauer, 2016), there are several removal treatments, including the three upon which this study is based: plots with mycorrhizal dicotyledonous herbs (called forbs henceforth), plots with grasses (all are mycorrhizal), and plots where mixtures of these two groups are retained (only the non-mycorrhizal species were removed). For simplicity, we use throughout the whole text the term **monoculture** for all plots where only one functional group is present, even though these plots contain multiple species in varying proportions.

We tested the following hypotheses. (H1) Due to possible compensation among the two functional groups, the temporal variability of the mixture is lower than the variability of individual functional

groups growing in monocultures. (H2) The temporal variability of individual functional groups (i.e., of forbs and grasses) in the mixture is enforced by the effect of competition of the other group, and thus it is higher in the mixture than in their respective monocultures. (H3) Due to compensatory dynamics, the temporal biomass variability of the grass–forb mixture is lower than the variability of the total of grass and forb monocultures. (H4) Whereas there might be both positive and negative temporal correlations between grasses and forbs across the years, the correlation between grasses and forbs growing together is – due to their mutual competition – more negative or less positive than the temporal correlation of their biomass values in monocultures. (H5) The temporal variability of individual replicate plots is positively correlated, and the correlation is higher for plots of the same functional group.

2 | METHODS

2.1 | Field sampling

Data were collected from permanent experimental plots at a study site near Zvíkov village, 10 km E of České Budějovice, Czech Republic (48°59′20″ N, 14°36′28″ E, 500 m a.s.l.). The soil type is a cambisol, with relatively low concentrations of nutrients (0.22 mg NH₄⁺, 0.06 mg NO₃[−], and 0.38 mg of inorganic extractable phosphates per 100 g of dry soil from the A horizon). This is an oligotrophic, traditionally managed meadow with a single mowing term in June, with high species richness (ca 85 higher plant species in all the experimental plots together) and some variation in its composition across the site. In the area of the field where the experimental plots are located, the six most abundant species are *Holcus lanatus*, *Plantago lanceolata*, *Sanguisorba officinalis*, *Anthoxanthum odoratum*, *Alopecurus pratensis* and *Poa pratensis*, accounting for approximately half of the total above-ground biomass at the time of mowing (see also Appendix S1 for more details). The nomenclature of plant species follows Kubát et al. (2002).

The original experimental design focused on comparing the roles that grasses and forbs play as hosts of arbuscular mycorrhizal fungi and consequently we distinguished three groups of vascular plants: mycorrhizal forbs (all C3 species, perennial species represent more than 99% of biomass), mycorrhizal graminoids (all being C3 perennial grasses in our area), and non-mycorrhizal species (six forb species and four sedge species). Having now available a long-time temporal series of data, we are able to analyze the temporal stability and synchrony of community components. The experiment, described in detail in Šmilauer and Šmilauerová (2013), was established in the form of 10 complete, randomized blocks, laid out in five columns and two rows, with the columns running along a perceived gradient of nutrient availability and rows along a perceived gradient of water availability. Within each of the blocks, four plots of different types were established, each 1 m × 1 m in size. We use three plot types in this study: (a) mixture plots containing both mycorrhizal forbs and mycorrhizal grasses, i.e., where only the non-mycorrhizal species were removed by weeding; (b) forb monoculture plots with only the

mycorrhizal forbs retained and all other species weeded out; and (c) grass monoculture plots with only (mycorrhizal) grasses retained and all other species weeded out (for species composition of the individual groups, see Appendix S1; pictures of individual plot types are in Appendix S2). In the experiment, there was also a fourth type of plots, without any removal at all. This control is not used here, because we do not have plots with non-mycorrhizal species only, which would be needed for a meaningful comparison. All the plants remaining in the experiment are mycorrhizal and thus, the effect of mycorrhizae cannot be considered in our analysis at all; however, because the non-mycorrhizal species are removed from all the plots, all plots are subject to some level of disturbance by (re-)weeding. The extent of soil and plant disturbance was substantially larger in the monoculture plots, as more species were removed compared to the mixed plots during the initial preparation of plots in 2001 and 2002. However, further weeding in subsequent years imposed similar levels of disturbance on all three plot types. The initial weeding took place in 2001 (blocks 1–6) and 2002 (blocks 7–10), with subsequent weeding performed 3–4 times every year since then. In addition, we cut the perimeter of each plot with a knife to a depth of 15 cm each spring and autumn to sever most of the rhizomes or roots growing into those plots from the surrounding sward.

The above-ground biomass was collected yearly from 2006 to 2016, as well as in 2004 and, for the first six blocks, in 2002 also. Biomass was collected from a central square (0.5 m × 0.5 m) in each plot in early June, cutting the stems approximately 1 cm above ground level to simulate traditional hay cutting and preserve regenerative buds. Biomass was not sorted to species level for every year, so for the purpose of the present study, we work with grasses and forbs, as data on these functional groups are available across all years and the experimental manipulation took place on the same taxonomic level.

2.2 | Data analysis

First, we characterized the temporal variability of each component (either total biomass of the plot, or biomass of a functional group) by CV (SD/mean, calculated both for each plot over the period of 13 years for the first six blocks and for 12 years for the remaining blocks, where data from 2002 are not available). Second, we estimated the synchrony between pairs of functional groups within plots or between pairs of plots using the Pearson correlation coefficient (calculated over the time series). Values of the Pearson correlation coefficient range from –1 (perfect negative correlation) to 1 (perfect synchrony). Biomass values for calculation of correlation coefficients were log-transformed to improve the two-dimensional normality, assumed for the correlation coefficient. The CV and correlation coefficients were then used as response variables in individual analyses tailored to test specific hypotheses. The design of the experiment enabled us to test the following hypotheses:

Hypothesis 1: The temporal variability of the total biomass in the mixture plots is lower than the variability of monocultures. We used the temporal CV for

each plot (i.e., forb monoculture, grass monoculture, or mixture plot) as the response variable in a randomized block ANOVA (i.e., type of plot as a fixed factor and block as a random factor). Then, we tested the planned contrast between the monocultures and the mixture. Because the community might be stabilized by high mean biomass (Gross et al., 2014) and significant transgressive overyielding in our system was already demonstrated for a shorter time period by Šmilauer and Šmilauerová (2013), we repeated the whole procedure also for the biomass averages, and also for the standard deviations calculated for each plot across all years.

Hypothesis 2: The variability of each of the components (i.e., grasses, forbs) is higher in the mixture than in the respective monocultures. We used the temporal CV at each plot as a response variable in a factorial ANOVA with grasses vs forbs, and mixture vs monoculture as fixed factors and block identity as a random factor. Whereas only the mixture vs monoculture effect is directly related to our working hypothesis, it is also interesting to know the difference in variability between the two functional groups (and eventual interaction between the two effects), provided by the ANOVA results.

Hypothesis 3: The temporal variability of the sum of biomass values from the forb and grass plots is higher than the variability of the biomass in the mixture, because in the mixture, the variability of the total biomass is determined by the physiological responses of the two groups (as is also the case for the sum of monocultures), but it is then decreased by a competition-induced asynchrony between the two functional groups. For each block, we calculated CV for the total biomass in the mixtures, and then CV for the sum of the biomass in the two monocultures in that block. These CV values were the response in a randomized complete block ANOVA (one fixed factor mixture vs monoculture, one random factor block; this model is equivalent to a paired *t* test).

However, this test compares the variability of a sum of two plots (which is also affected by spatial asynchrony that can stabilize the sum) with the variability of a single mixture plot, where this stabilization is not possible. To have a “fair” comparison, where the same spatial asynchrony will be in both monocultures and mixtures, we also compared the sum of two different monocultures from neighboring blocks with the sum of two mixtures. Thus, we used pairs of adjacent blocks and compared the variability of a sum of two mixtures (where the grasses and forbs are in competition) and the sum of two different monocultures, where the functional groups do not compete. There are two possibilities of choosing a combination of

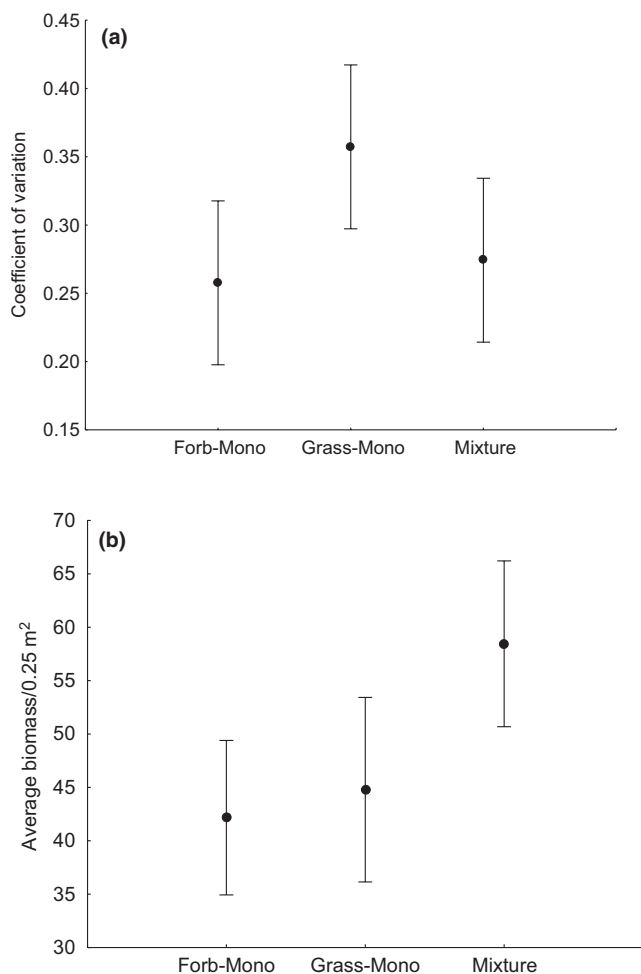


FIGURE 1 (a) Average values of CV for the biomass in the Grass monocultures, Forb monocultures and Mixtures. The randomized complete block ANOVA shows marginally significant differences ($F_{2,18} = 3.49$, $p = 0.052$), but the contrast between Monocultures and the Mixture is not significant. (b) Average biomass in the Grass monocultures, Forb monocultures and Mixtures. The randomized complete block ANOVA shows highly significant differences ($F_{2,18} = 14.6$, $p < 0.001$), with highly significant contrast between monocultures and the mixture ($F_{1,9} = 20.01$, $p = 0.0015$). The error bars show the 95% confidence intervals

forb monoculture and grass monoculture for each pair of blocks, so we calculated the variability of each pair. In this way, both values are composed of two plots (originating from different blocks), and thus both are affected by the same environmental variability. While there are more possibilities how to pair various blocks, their inclusion would mean that the same data were used several times, violating the assumption of independent observations. The data were analyzed by randomized block ANOVA. Each computational block was formed by two adjacent physical blocks in the field, and contained one value for sum of mixtures and two values for sum of monocultures.

Hypothesis 4: The temporal correlation between grasses and forbs is higher (i.e., more positive or less negative) when calculated for the monocultures of the

same block than for the two components of the mixture plot in the same experimental block. Moreover, we expect that the correlation between monocultures will be mostly positive (because it is mainly driven by weather fluctuations) whereas in mixtures, the negative correlation might be caused by competition between grasses and forbs. For each block, we calculated the grass–forb correlation coefficient for monocultures and mixtures, and these correlation coefficients were the response in a randomized complete block ANOVA (with the same predictors as in Hypothesis 3).

Hypothesis 5: The temporal correlation between all the monoculture plots is mostly positive, as they are driven by the same weather fluctuations. However, we expect stronger (more positive) correlations between pairs of plots representing the same functional group (i.e., either grass–grass or forb–forb comparisons), because each group is characterized by a slightly different physiological response to weather fluctuation, than between pairs from different groups (grass–forb). If synchronization is stronger under similar soil conditions, and plots within a block are more similar to each other, then the within-block correlations should be higher than those across the blocks.

For all 20 plots with monocultures (i.e., 10 grass and 10 forb plots), we calculated temporal correlations, yielding 45 grass–grass correlations, 45 forb–forb correlations, and 100 grass–forb correlations. Nevertheless, the individual values are not independent, and so they cannot be compared by a simple ANOVA or similar models. Therefore we converted the matrix of correlation coefficients into a matrix of distances, defined as $distance = 1 - correlation$ to avoid negative distances. Thus, perfectly positively correlated plots would have a zero distance, pairs of plots without correlation would have distance 1, and negative correlations will result in a distance value higher than 1. We then calculated the distance-based RDA (db-RDA, Šmilauer & Lepš, 2014), with the grass/forb and block identity as the explanatory variables. If there is a larger positive correlation between plots of the same functional group, then the grass/forb explanatory variable should have a significant effect; if there is a synchronizing effect of block, then the block predictor should have a significant effect. Visual inspection of the ordination diagram also permits comparison of the variability within grass plots and within forb plots.

3 | RESULTS

Hypothesis 1: The differences in CV for the total biomass among the three categories of plots were

marginally significant ($F_{2,18} = 3.49$, $p = 0.052$, Figure 1a) – the grass monocultures were the most and the forb monocultures the least variable, whereas the temporal variability of the mixtures was slightly higher but close to that of the forb monocultures. The contrast between the monocultures and the mixtures was not significant. Using multiple comparisons (Tukey), only the difference between grass and forb monocultures was marginally significant, ($p = 0.059$). At the same time, the mixture is significantly more productive than both the monocultures ($F_{2,18} = 14.6$, $p < 0.001$, Figure 1b), with a highly significant contrast between monocultures and the mixture ($F_{1,9} = 20.01$, $p = 0.0015$). The difference of productivity between the two monocultures was not significant. The differences between standard deviations ($F_{2,18} = 3.73$, $p = 0.044$; Appendix S3) followed the order of mean biomass value.

Hypothesis 2: Temporal variability (CV) of each functional group was higher in the mixture plots than in the corresponding monocultures, and the variability of grasses was higher than the variability of forbs (Figure 2). The effects were additive, as their interaction was not significant.

Hypothesis 3: Temporal variation (measured as CV) for the total biomass of the mixture and for the sum of monoculture biomass values was nearly identical ($F_{1,9} = 1.149$, $p = 0.312$). In fact, the CV for the mixture was slightly higher (0.289) than for the sum of monocultures (0.249). When we summed up the neighboring blocks, the average CV of mixtures (expectedly)

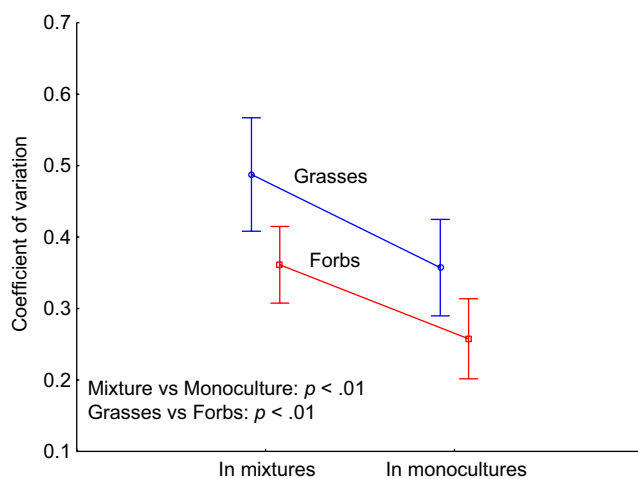


FIGURE 2 The average values of CV (over ten blocks) for the biomass of forbs and grasses in mixtures and in monocultures. The main effects are significant (grasses vs forbs: $F_{1,9} = 13.78$, $p = 0.005$, mixture vs monoculture: $F_{1,9} = 17.50$, $p = 0.002$, their interaction is not significant $F_{1,9} = 0.20$, $p = 0.66$). The error bars show the 95% confidence intervals

decreased (0.246), whereas the variability of sums of monocultures remained nearly the same, practically identical with the variability of sum within block (0.235), and the difference between the CV of sum of monocultures and mixtures was clearly non-significant ($F_{1,4} = 0.07$, $p = 0.806$).

Hypothesis 4: Temporal correlation between grass and forb biomass values is higher between monocultures than in the mixture plots in all blocks except one (Figure 3). Moreover, the average correlation between monocultures is positive (average $r = 0.197$, the 95% confidence interval CI is $[-0.022, +0.416]$, i.e., the lower limit of the 95% confidence interval for the mean is negative but very close to zero), whereas the average correlation in the mixture is significantly negative (average $r = -0.307$, CI $[-0.602, -0.012]$).

Hypothesis 5: The monocultures across blocks are much better correlated if they belong to the same functional group: the average correlation coefficient between two forb plots is $r = 0.444$, and between two grass plots is $r = 0.417$ – average across 45 pairs in both cases, whereas the average of all 100 possible grass–forb monoculture pairs is $r = 0.124$ (Figure 4). Accordingly, the db-RDA (Appendix S4) shows a highly significant effect of the grass/forb factor, but no significant effect of block. This suggests differing responses of grasses and forbs to inter-annual weather fluctuation, but generally no effect of spatial proximity on the similarity of plot responses to weather fluctuations.

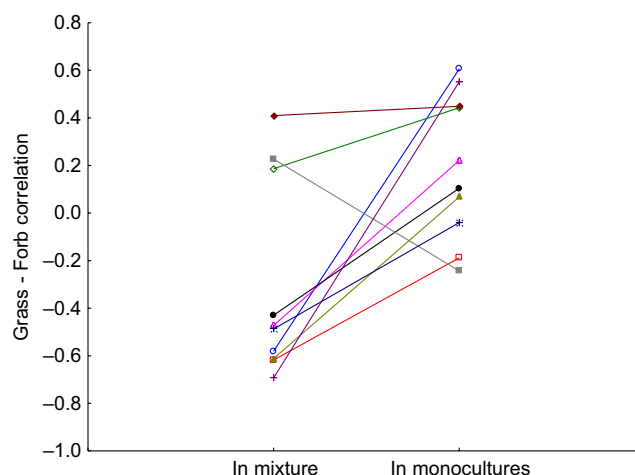


FIGURE 3 Values of correlation coefficients between the forb and grass log-transformed biomass in mixture plots and between monoculture plots. The corresponding values from the same block are connected by lines. The average values of correlation differ between the mixture and monoculture plots ($F_{1,9} = 9.87$, $p = 0.012$)

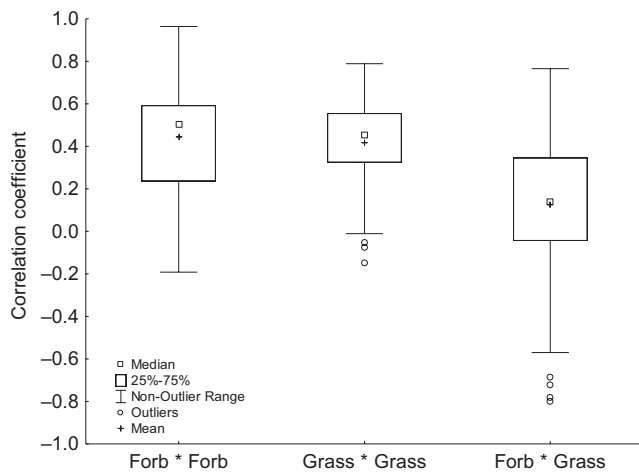


FIGURE 4 Box and whisker plot of the Pearson correlations between all possible pairs of Forb monocultures, of Grass monocultures, and the pairs of Grass and Forb monocultures. The test using distance-based RDA has shown that the values of correlation coefficients are significantly higher between plots with the same functional group (see Appendix S4 for details)

4 | DISCUSSION

Our time series does not show a pronounced stabilizing effect of the presence of both functional groups in a common mixture, since the variability of whole-mixture-plot biomass is between the variability of plots with either forbs or grasses. Even though it is closer to the variability of forbs, which are the most stable, and thus lower than the average of variability of monocultures, the difference is not significant. Also, the variability of the sum of monocultures is nearly the same as the variability of the mixture (in fact slightly lower). On the contrary, the results clearly show that when the two functional groups are in competition (in mixture plots) each functional group fluctuates more than when growing alone. This increased variability in the mixture supports the hypothesis of destabilizing effect of competition on individual components (Loreau & de Mazancourt, 2013; Tilman, 1996; van Ruijven & Berendse, 2007). The temporal correlation between the biomass of grasses and forbs growing separately is on average weakly positive (corresponding similarities in their physiological responses), whereas within the mixture, they are negatively correlated, which is a strong indication of an asynchronizing effect of competition, in concordance with findings by Loreau and de Mazancourt (2013) and Tilman (1996).

Our results suggest that we need competition to achieve the negative correlation (i.e., compensatory dynamics). This confirms the conclusions based on analyses of a wide range of sowing experiments from grasslands, by Gross et al. (2014; their Analysis 3), whereas their results for algal communities were much weaker. This shows the robustness of these results, because they are similar for sowing and removal experiments but depend more on the nature of the system (grasslands vs algae). The stabilizing effect of competition on the total biomass was not proved despite increased asynchrony

and despite demonstrated overyielding of the mixture, which should also stabilize the mixture biomass (de Mazancourt et al., 2013). This suggests that in our case, the asynchrony, together with the increased total biomass in mixture, is just sufficient to compensate for the destabilizing effect of competition on individual community components. Nevertheless, the average correlation between monocultures of the same type was below 0.5, showing that the spatial asynchrony is an important factor stabilizing the biomass with increasing spatial scale (Wang & Loreau, 2014).

The temporal correlation between pairs of monoculture plots belonging to the same functional group is considerably higher than the correlation of monocultures belonging to different functional groups (nevertheless, even the latter correlation is mostly positive). The significantly more positive correlation for plots of the same functional group signifies that the physiological reaction to weather fluctuation is different in the two groups, but the overall prevalence of positive correlations, also for plots with different functional groups, confirms that, despite differences, the similarity in response to weather conditions prevails.

The theory about a competition effect was developed for individual populations (Tilman, 1996), whereas we used functional groups. Yet we believe that a similar reasoning can be used in both cases. In fact, not the populations (species), but the individuals (individual ramets) compete with each other. The growth of individuals in a two-species mixture is affected by both intra- and interspecific competition, the growth of individuals in a monospecific situation is not competition-free either, but is affected only by intraspecific competition. Similarly, in our case, the growth in a single functional group is affected by the competition of individuals of the same functional group, and in mixture plots by competition of individuals of both the same and the other functional group. The basic assumption here is that the individuals within the same class (i.e., within a species, or within a functional group) are on average functionally more similar than between the groups. This is undoubtedly true for grasses vs forbs, which differ in numerous functional traits important for community processes (Díaz & Cabido, 2001; Symstad & Tilman, 2001). This is also why these functional groups were used in the biodiversity experiments from their very beginning (e.g. Biodepth – Hector et al., 1999; CLUE – Van der Putten et al., 2000; Jena experiment – Roscher et al., 2011). Finally, the temporal correlations being significantly higher among the monocultures of the same functional group than the correlations between monocultures of different functional groups clearly demonstrate the functional differences between those two groups.

The largest difference in temporal variability was found between grasses (exhibiting larger temporal fluctuation of biomass) and forbs, regardless of whether they grow separately or in a mixture with one another. Both in monocultures (Figure 1a) and in mixtures (data not shown), the biomass of grasses is slightly (but not significantly) higher than that of forbs, so that the difference cannot be caused by increased mean biomass. The two groups are functionally very distinct, with large differences in important functional traits, including the root system, leaf morphology, etc., so we can only speculate

which of these differences is important for temporal stability. The ability of forbs to quickly mobilize stored reserves after hay cutting or after a period of summer drought is readily observed when their new above-ground biomass temporarily dominates the sward. This result supports the idea that the life history of individual species or functional groups is one of the important determinants of stability (Lepš et al., 1982; MacGillivray & Grime, 1995; Májeková et al., 2014).

In principle, it is also possible that the higher stability of forbs is caused by their slightly higher species richness. However, the data do not support this explanation, as the effective number of species (expressed either as the antilogarithm of Shannon H' or the reciprocal of Simpson dominance – unpublished data from biomass in a single year) is roughly the same for both groups. More likely, forbs include a morphologically and phylogenetically heterogeneous group of species, containing ranunculids, rosids and asterids, whereas grasses are a single, morphologically and functionally homogeneous family Poaceae. The phylogenetic diversity is considered to be a good proxy for the functional diversity, and a sometimes better predictor of ecosystem functioning than functional diversity based on a limited number of traits (Cadotte, Cardinale, & Oakley, 2008). The phylogenetic diversity of forbs is undoubtedly much higher than that of grasses – the ranunculids split from rosids and asterids ca. 270 million years ago, whereas the grasses started to diversify slightly more than 50 my ago (Durka & Michalski, 2012). Most studies, particularly where diversity was manipulated, demonstrate that functional diversity stabilizes total biomass (Roscher et al., 2011), and this might also be the case here. The higher species richness of mixtures in comparison with both monocultures (Šmilauer & Šmilauerová, 2013) and large differences between the two functional groups imply that not only species richness, but also the functional diversity of the mixture is much higher than that of the monocultures, whatever metrics are used; still, the CV of forbs is (non-significantly) lower than the CV of the mixture. Nevertheless, neither taxonomic nor functional or phylogenic diversity can explain why is the spatial synchrony within group is higher than between groups and thus it seems that the functional differences between forbs and grasses are the most important cause of their differences in temporal stability.

In the majority of cases, the correlation coefficients were rather low, showing a low level of synchrony. For the case of two components, the value of the correlation coefficient is identical to the values of the Gross et al. (2014) synchrony. This is true regardless of whether the weighted or unweighted form was used (Lepš et al., 2018) as weighting does not play a role if there are just two components. Perfect synchrony (corresponding to a correlation coefficient value +1) among the individual components of a community is in reality not achievable. Each individual is independent and thus reacts slightly differently to the same weather fluctuation. Moreover, the omnipresent small-scale environmental variability within each plot can cause individuals to experience slightly different conditions, which are likely to further decrease synchrony. From a plant's point of view, the variability in underground conditions also includes the variability of soil biota, which might fluctuate in both space and time.

Demographic stochasticity (Anderson, Gordon, Crawley, & Hassell, 1982) also leads to deviation from perfect synchrony. Because we work in a mown meadow, and thus the biomass can be taken each year from exactly same location, we were able to minimize the sampling error, which might otherwise affect the estimates of variability and asynchrony (de Mazancourt et al., 2013).

Aside from these basically stochastic events, asynchrony can be caused by two sets of factors – the first is the differences in the physiological response between individual components (e.g., different species have different physiological responses to weather fluctuations, and the same will probably be true for different functional groups). However, in this case, we can still expect some positive correlation as, for example, a shortage of water is physiologically unfavorable for all species. Our data support this expectation, as the average grass–forb correlation in monocultures is still (weakly) positive. The second set of factors forms the ecological response, i.e., the response of a component when in a community, where it encounters competition with others, might be rather different. Differences between physiological and ecological responses to environmental gradients have been demonstrated many times (Austin & Smith, 1989; Ellenberg, 1988), and we can speculate that differences between the physiological and ecological responses to weather fluctuations might also be very pronounced. Water shortages can harm acquisitive dominants greatly, while slightly stress-tolerant subordinate species can even react positively due to a reduction in competition (but we are not aware of any data supporting this speculation). Our data show that while the physiological response produces positive correlations (i.e., the response is similar in the two components), for the dynamics governed by the ecological response, i.e., in a mixture, negative correlations prevail. This shows that the eventual compensatory dynamics is most likely the consequence of competition between community components. Similarly, Gross et al. (2014) found negative synchrony also only in competitive situations.

The (a)synchrony of components in an intact community reflects the ecological response to weather fluctuations, i.e., the combined effect of the physiological response and competition. From our data, we can roughly estimate the effect of individual components governing the synchrony of forbs and grasses in the community. The average temporal correlation of plots of the same functional group (i.e., plots reflecting the same physiological response) is between 0.40 and 0.45 – this shows that their synchrony is far from perfect, and suggests that stochastic effects play an important role in decreasing synchrony. This corresponds well to the concept of decreasing temporal variability with spatial scale (Wang & Loreau, 2014; Wang et al., 2017) – the low level of synchrony, even between plots of the same type in close proximity, suggests that we can expect rapid stabilization of fluctuations (i.e., of CV) when we increase the area of sampled plots. Nevertheless, the fact that synchrony is not weaker between blocks than within blocks does not provide strong support for the idea of spatial decay of correlations (Wang & Loreau, 2014). This may result from the fact that all of the plots are rather close to each other, on a scale of tens of meters. The differential or asynchronous physiological response of different species to environmental



fluctuations is expected to be one of the most important stabilizing factors of total community biomass (Gonzalez & Loreau, 2009), even though the empirical support is not very strong (de Mazancourt et al., 2013). However, the difference in physiological response is significant (Figure 4), but not strong enough to have sufficient stabilizing effect.

Our data suggest that even with the stochastic variability and differences in physiological response, we still see a prevalence of weak positive correlations between monocultures of different functional groups. Our data suggest that compensatory dynamics (i.e., prevalence of negative correlations among components) can only be achieved when the two components are in competition.

Even though the temporal correlation between forbs and grasses growing in mixture is significantly negative and lower than that of monocultures, the CV of the sum of monocultures is even slightly (non-significantly) lower than the CV of the mixture. We were thus not able to confirm our hypothesis 3. We expected that this might be due to the effect of spatial insurance (Wang & Loreau, 2014) – i.e., the effect of spatial variability, which affects the sum of two monocultures, but not the mixture. Nevertheless, when we paired the mixtures and the monocultures of adjacent blocks, the effect of spatial insurance is exactly the same for the pairs of monocultures and the pairs of mixtures: the CV of the two groups is nearly identical, but still (negligibly) lower for the monocultures.

We have used functional groups and not the individual species used in the theories. In our view, the effect of competition on the variability of individual community components can only be shown when the individual components' variability is available, when they are grown separately and in mixture. This necessarily requires diversity manipulation (either by sowing with subsequent weeding or by removal). We consider the removal experiments to be much closer to real plant communities than the experiments sowing various species mixtures (Diaz et al., 2003). First, the species composition contains only species (and genotypes) that were already proved to be able to coexist there (otherwise they would not be part of the original community). Second, the soil organisms there are those that have already interacted with the plant species, very probably for many years. As far as we know, our data are the only removal experiment where the two components and their mixture have been available for more than 10 years, thus enabling reliable estimates of variability and synchrony. We are aware that there is very probably some stabilization within functional groups, caused by the asynchrony of individual species within functional groups (Lepš et al., 2018). Thus, we are not able to decide unequivocally whether the lower variability of forbs is due to a higher stability of their individual species, or because this group is more (functionally) diverse. However, the fact that the two components show compensatory dynamics in mixture and are slightly positively correlated when growing separately is a clear demonstration of the competition effect, independent of possible within-group compensation. Similarly, the significantly higher correlation among plots with the same functional group demonstrates the differential response of forbs and grasses to weather, again independently of possible within-group compensation.

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AUTHOR CONTRIBUTIONS

JL conceived the ideas and led the writing of the manuscript. MŠ and PŠ designed, carried out and maintained the long-term experiment, including data acquisition. JL and PŠ analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available in the digital Supporting information as Appendix S5 (data description), and Appendix S6 (data).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1. Overview of important species within the two groups (forbs and grasses), based on above-ground biomass sampled in June 2010

APPENDIX S2. Pictures of the forb monoculture, grass monoculture, and mixture three years after the start of the experiment

APPENDIX S3. Average values of temporal standard deviation for the biomass in the grass monocultures, forb monocultures, and mixtures

APPENDIX S4. Biplot with the first two axes of the distance-based RDA, calculated from the temporal correlations between above-ground biomass of individual plots with grass or forb monocultures

APPENDIX S5. Description of primary data stored in Appendix S6

APPENDIX S6. The primary data in pdf and csv formats

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