Variability in population and community biomass in a grassland community affected by environmental productivity and diversity

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Temporal variability of the biomass of individual populations and total community biomass were studied in a species rich meadow (35–40 species 0.25 m^{-2} plot). Communities were experimentally subjected to fertilization and removal of the dominant *Molinia caerulea* in a factorial design. The typical dominance structure, with few dominants and many sub-ordinate species, developed in all the treatments. Variability was measured by the coefficient of variation between years, from the fifth to the eighth year of the experiment (to avoid the initial response to the manipulations). Dominant removal increased the diversity measured by the reciprocal of the Simpson index, while fertilization decreased both species number and diversity and also caused a shift in community composition. The variability of both the total community and of individual species was higher in the fertilized plots. The coefficient of variation decreased with species mean biomass in all the plots. In non-fertilized plots, the dominant species had lower variability than total biomass. The biomass values of individual species fluctuated in a concordant manner over the years (i.e. were positively correlated). All of these factors will decrease the strength of the expected portfolio effect. It is argued that the effect of environmental productivity on variability is more pronounced than the effect of diversity.

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The idea that diversity begets stability has been prevalent in ecological literature for a long time (Odum 1953, Elton 1958). For example, the well-known Shannon Wiener index of diversity H′ was introduced to ecology by MacArthur (1955) as an index of stability. The idea behind it was that, if there were more redundant species in a community, the failure of one of them could be compensated for by the other species present. In fact, this is a mechanism, which roughly corresponds to what is today known as the portfolio effect (Doak et al. 1998, Tilman et al. 1998). Various mechanisms leading to increasing stability with increasing diversity were suggested (Yachi and Loreau 1999, McCann 2000, Loreau et al. 2002), however, all are (explicitly or implicitly) based on the differential response of species to environ-

mental fluctuation. A competing view, however, suggests that the life-history characteristics of the constituent species, and particularly of dominants, are the most important determinants of community functioning, including its stability (Lepš et al. 1982, MacGillivray et al. 1995, Wardle et al. 2000, Grime 2001).

Completely different view was presented in May's (1973) classic book. May used mathematical models to show that stability should decrease with system complexity. However, a closer look shows that, in fact, there is a decrease in the probability that the equilibrium of a system with randomly generated interaction coefficients will be stable a in Liapunov sense. How simple models with randomly generated coefficients correspond to ecological reality and what is the relationship between

the mathematically defined Liapunov stability and ecological concepts of stability (Harrison 1979) remains open to question (discussion in May's book).

In his seminal review of the diversity–stability relationship, Pimm (1984) showed that there are various meanings of stability and various measures of diversity (and, consequently, many various combinations of those two). Consequently, the question about the relationship of those two could be answered only when we are able to provide operational definitions of diversity and stability, and define the way how to measure them.

In this paper, we will examine one character of stability, temporal variability, measured by the coefficient of variation (CV = standard deviation/mean). Further, we will distinguish between population variability and community variability, based on the biomass fluctuation among years, as suggested by Micheli et al. (1999). These two measures might be very different; total community biomass may be fairly constant despite pronounced individual population fluctuations. This is exactly what the portfolio effect predicts (Doak et al. 1998, Tilman et al. 1998). If X_1, X_2, X_3, ..., X_k are independent random variables with the same mean and variance, representing biomass values of all the species in a community (note that if the variables are independent, then the species have to respond differentially to environmental variation), then

$$CV_{community} = \frac{CV_{species}}{\sqrt{k}}$$

where k is the number of constituent species. The effect is strengthened by a negative (temporal) correlation between species, and weakened by a positive correlation between species. The concordant response of individual species to environmental fluctuation produces a positive correlation, whereas niche complementarity together with competition is expected to lead to a negative correlation (Lehman and Tilman 2000). When we expect a constant $CV_{species}$ and species of different abundance, then the effect is weaker the more species abundances differ. However, the $CV_{species}$ is often not constant and decreases with species abundance, depending on how the variance is scaled with the mean. The relationship between the variance and mean has been long known in ecology as Taylor's power law (Taylor 1961)

$$log(variance) = a + b \, log(mean)$$

where a and b are parameters (intercept and slope), fitted usually by means of regression. If b = 2, then CV is independent of the mean. The portfolio effect weakens with decreasing b, and disappears for b = 1 (Cottingham et al. 2001).

Lehman and Tilman (2000), investigating the competition models, have demonstrated that increased species diversity should lead to lower variability of compound community characteristics (like total biomass), because

of the portfolio effect, but the variation of individual populations is amplified by competition and is expected to increase with species diversity. This is in very good agreement with the empirical results of Tilman (1996).

The assessment of temporal variability in real communities is complicated by spatial heterogeneity. When we estimate the biomass of a plot based on a randomly selected sample of sub-plots, then the standard error of estimate is (with constant sample size) dependent on the spatial heterogeneity. Consequently, any assessment of temporal variability will be confounded by spatial heterogeneity of the community (Cottingham et al. 2001). In mown meadows, we can use the clippings (with subsequent collection of the mown biomass) as a measure roughly equivalent to mowing. In this way, we obtained biomass from permanently marked plots. Then, the variability between years is not confounded by spatial heterogeneity.

In an experiment in permanent seminatural meadows, we created four community types by fertilization and dominant removal in a factorial design. The removal of the dominant changed the population structure, but not the total productivity, whereas fertilization changed both population structure and also fertility. Based on the temporal sequence data from these communities, we aimed to answer the following questions:

1. Is variability affected by the presence of the dominant species and by fertilization?
2. How is the temporal variance scaled with the mean?
3. Is the variation of individual species correlated in time?

Based on the comparison of variability of species and total community biomass under various treatments, we wanted to test the predictions of various models of the functioning of the portfolio effect. Also, we compared the importance of diversity and environmental productivity as determinants of community stability by comparing the effect of dominant removal and fertilization.

Methods

Study site

This study was conducted in a species rich wet meadow (Molinion with some species of Violion canine according to the phytosociological classification) located 10 km south-east of České Budějovice, Czech Republic, 48°57′N, 14°36′E, 510 m a.s.l., close to the village of Ohrazení. Mean annual temperature is between 7 and 8°C, and mean annual precipitation is 600–650 mm. Traditional meadow management consisted of regular mowing occurring once or twice a year. This was stopped at the end of the 1980's and the meadow was not mown

again until the start of the experiment in 1994. The community is dominated by a tussock grass *Molinia caerulea*. Other common grasses are *Anthoxanthum odoratum*, *Nardus stricta*, *Agrostis canina*, *Briza media*, *Festuca rubra*, *Holcus lanatus*, *Danthonia decumbens* and a number of sedges, e.g. *Carex panicea*, *C. palescens*, *C. leporina* and *C. hartmanii*. The most common herbs are *Myosotis nemorosa*, *Potentilla erecta*, *Prunella vulgaris*, *Lathyrus pratensis*, *Cirsium palustre*, *Galium uliginosum* and *Lysimachia vulgaris*.

Experimental design

In 1994, 24 permanent plots, 2×2 m each, were established in the meadow. The plots were sampled before three treatments (fertilization, mowing, and removal of the dominant species, *Molinia caerulea*) were started. The fertilization treatment consisted of annual application of 65 g m^{-2} of a commercial NPK fertilizer (12% N (nitrate and ammonium), 19% P (as P_2O_5) and 19% K (as K_2O)), applied in two dosages, 50 g m^{-2} in autumn and 15 g m^{-2} in spring (starting in 1997 the total dosage was applied only in spring). The mowing treatment was annual scything of the quadrats in June, with removal of the cut biomass after mowing. *Molinia caerulea* was manually removed by screwdriver in April 1995 with a minimum of soil disturbance. New individuals were removed annually. Biomass was recorded annually. In the mown plots, the biomass in the central 0.5×0.5 m was clipped prior to mowing, separated into species, oven-dried and weighted (non-mown plots are not used in this paper). The design and results from the first four seasons are described in detail in Lepš (1999).

The community is very species rich (up to 35 to 40 species per 0.5×0.5 m plots in the non-fertilized treatments). Identification of sterile shoots was extremely difficult for some species. For analysis, misidentifications could be dangerous, because they would cause a spurious negative correlation (the biomass subtracted from one species would be added to another one). Consequently, for a few species where we were not completely sure, we pooled similar species for analysis (e.g. *Carex umbrosa* and *C. pilulifera* were pooled).

This paper is based on the biomass data from 1999–2002. The first five years (baseline and the first four years after the treatments started) were omitted, because during them vegetation dynamics were governed by directional responses to the treatments, whereas during the analyzed period the directional changes were small.

Data analysis

For each plot, the mean, variance, standard deviation, and coefficient of variation were calculated for each species biomass and for the total biomass. Based on the data for individual species, we calculated the regression of log(variance) on log(mean), yielding the parameters a and b for each plot. Then the sum of variances of individual species' biomass were compared with the variance of community biomass. If the species fluctuate independently, then the two values should be the same. A higher variance of community biomass means concordant variation (positive correlation), while a higher sum of the species' variances means a negative correlation.

The diversity of individual samples was characterized by the number of species and by the Simpson dominance index:

$$\text{Simpson} = \sum \left(\frac{N_i}{N} \right)^2 \quad N = \sum N_i$$

where N_i is the biomass of i-th species. The Simpson index takes into account both the number of species and their proportions. High values of the index mean low diversity.

Results

Although the plots, particularly the non-fertilized ones, are very species rich, the bulk of the total biomass is formed by a very limited number of species. When summing all the three replicates in 2000, 90% of the biomass was achieved by 27 out of 57 species in the non-fertilized plots with dominant removed, 12 out of 47 in the removal fertilized plots, 23 out of 54 species in the non-fertilized control plots, and 8 out of 37 in the fertilized control plots. In the last case, the 14 least abundant species totaled less than 1% of the total community biomass.

Total biomass (Fig. 1, Table 1) fluctuated significantly among years and was higher in the fertilized plots. No
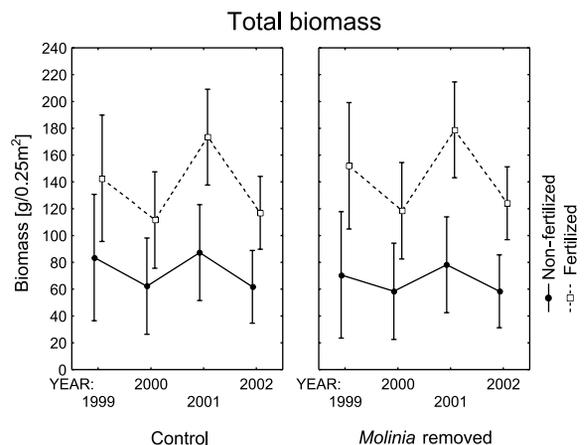
Fig. 1. The changes in total biomass during the years 1999 to 2002. The error bars denote 95% confidence intervals. Results of the repeated measures ANOVA are in Table 1.

Table 1. Results of the repeated measures ANOVA of the total biomass, and of the Simpson index. The main effects are fertilization (Fert), *Molinia* removal (Rem), and the repeated measures factor is year (Yr). × = interaction.

Effect	df effect	df error	Total biomass		Simpson index	
			F	p-level	F	p-level
Fert	1	8	31.608	$< 10^{-3}$	30.881	0.001
Rem	1	8	$< 10^{-3}$	0.997	5.463	0.048
Yr	3	24	11.022	$< 10^{-3}$	2.100	0.127
Fert × Rem	1	8	0.343	0.574	1.140	0.317
Fert × Yr	3	24	2.058	0.132	1.704	0.193
Rem × Yr	3	24	0.030	0.993	0.144	0.932
Fert × Rem × Yr	3	24	0.054	0.983	0.491	0.692

differences were found between the removal and control plots. (Because the differences between removal and non-removal plots are surprisingly small, we double-checked that the unlikely low F-values for removal are not a consequence of a computational error. We concluded that this happened just by chance.) Total biomass was well correlated with precipitation during April and May, i.e. roughly from the start of the growing season to the beginning of sampling. Precipitation values for 1999 to 2002 were 99.7 mm, 56.7 mm, 139.7 mm, and 41.4 mm respectively (average over the whole experiment, i.e. from 1994 to 2002, is 113.2 mm, all from the Ledenice meteorological station, ca 4 km from the experimental site). Species number was lower in the fertilized plots (P < 0.01), and decreased with time in the fertilized plots (significant year × fertilization interaction, P < 0.01). Species continued to become extirpated from the community in the fertilized plots even 8 years after the start of the experiment. No effect of removal was found. The Simpsons index (Fig. 2, Table 1) of dominance was fairly constant over the years. It was considerably higher in the fertilized plots and slightly higher in the controls compared to the removal plots.
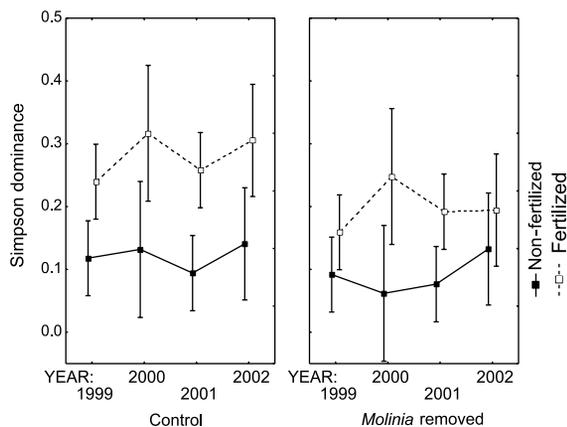
The variability of total biomass (characterized by CV) was slightly higher in the fertilized plots (Fig. 3, Table 2), but absolutely no difference in variability was found between the control and removal plots. Both the a and b parameters of the Taylor power law were significantly higher in the fertilized plots; parameter a also increased slightly with dominant removal (Fig. 4, Table 3). This shows that the variability of individual species biomass is considerably higher in the fertilized plots. This can be documented by the variability of common species (Fig. 3, Table 2). The values of the b parameter were between 1.5 and 1.7; meaning that the coefficient of variation decreased with species biomass (Fig. 5). Also, some of the species were repeatedly found below the regression line. This was typical e.g. for *Potentilla erecta*, and particularly for *Molinia caerulea*, the dominant species. By comparing the variability of *Molinia caerulea* with the variability of the whole community, it is seen that the variability of the dominant in the non-fertilized plots was even smaller than the variability of the total biomass (Fig. 6).

In ten out of the twelve plots, the variance of the total biomass is higher than the sum of variances of individual species. This suggests that, on average, the biomass variation is positively correlated over time. The closer inspection of the individual species variation shows that in the non-fertilized plots the dominant, *Molinia caerulea*, fluctuate much less than the remaining species.

Discussion

Unlike in most similar experiments, semi-natural communities were investigated. In particular, species composition of the non-fertilized control plots was typical for semi-natural oligotrophic meadows in the area. The species composition of these meadows has stabilized and developed over centuries of extensive meadow management. This is important, because species are able to coexist for long time under a given management. Also, not only the set of species, but the identity of dominants and sub-dominants corresponds to this type of meadows in the landscape. Unlike the other removal studies (Allen and Forman 1976, Wardle et al. 1999), this study does

Fig. 2. Changes in the value of the Simpson index (reciprocal value of the Simpson index is a measure of diversity) in the course of four years. The error bars denote 95% confidence intervals. Results of the repeated measures ANOVA are in Table 1.

Total biomass

Anthoxanthum odoratum

Festuca rubra

Potentilla erecta
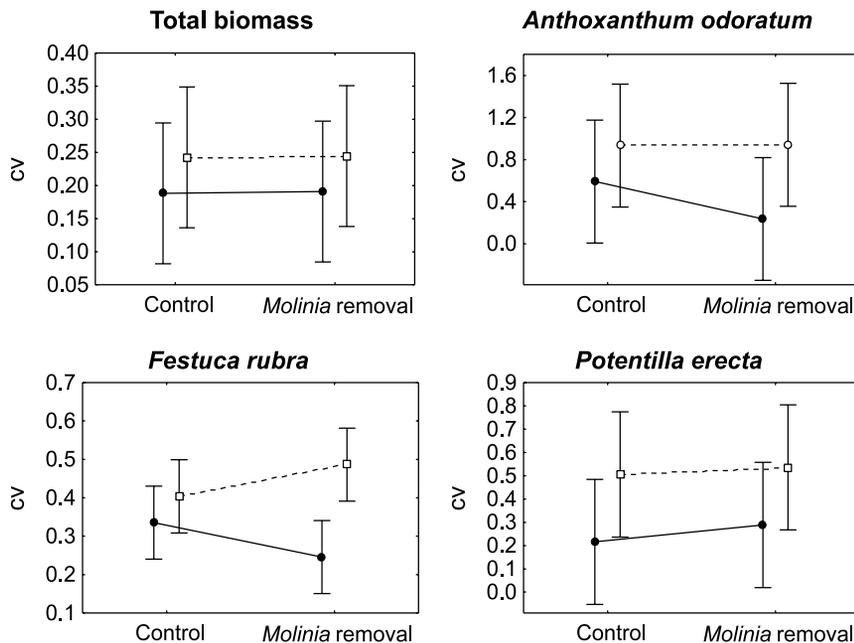
Fig. 3. Coefficients of variation for total biomass and selected common species. The error bars denote 95% confidence intervals. Fertilized plots are shown by open symbols and broken lines, the non-fertilized by full symbols and full lines. Results of the two way ANOVA are in Table 2.

not focus on the immediate reaction of the community. Instead, the first five years were omitted, and variability which is not influenced by the trend was studied. The typical population structure developed in all treatments, with a limited number of important species and a "tail" of rare species. The highly unequal distribution of species proportions decreases the strength of the expected portfolio effect (Fig. 3 in Cottingham et al. 2001). It is very unlikely that the species in the tail of the distribution (i.e. the species with negligible biomass) would be able to affect the total productivity of the community. Still, they form a relatively high percentage of the total number of species (in the fertilized control plots, more than one third of the species formed less than one percent of the biomass). Therefore, it seems that (the reciprocal of) the Simpson dominance index is a better characteristic of diversity than the plain number of species. Similarly, Wilsey and Potvin (2000) and Roy and Nijs (2000) stress the importance of evenness for ecosystem functioning.

By removing the dominant, total species richness did not change, but evenness in the community increased (and consequently, the Simpson index of dominance decreased). But with the exception of *Molinia*, neither the species composition, nor environmental conditions changed considerably. This is not a general feature of all removal experiments – in general, the removal can result in wide range of response types of the rest of the community (Allen and Forman 1976, Abul-Fatih and Bazzaz 1979, Hils and Vankat 1982, Díaz et al. 2003). Also note, that here, the state five years after removal is reported; during the first season after the removal, the removal plots had lower biomass (Lepš 1999). Fertilization caused decrease in diversity (whether measured by total number of species, or the reciprocal of the Simpson index), increase in productivity, and also a shift in the community composition.

Removal of the dominant had negligible (if any) effect on both the total biomass and its variability. Total biomass variability was higher in the fertilized plots (the effect was not significant, but the test was rather weak due to the low number of replications). The effect was in the "expected" direction, i.e. the less diverse fertilized plots exhibited higher variability. Similarly, Tilman and

Table 2. Two way ANOVA of coefficients of variation of the total biomass and of biomass of selected species. The main effects are fertilization (Fert) and *Molinia* removal (Rem). For both main effects and interaction ($\times$), df effect = 1, df error = 8.

	Total		Anthoxanthum		Festuca		Potentilla	
	F	p-level	F	p-level	F	p-level	F	p-level
Fert	1.358	0.277	4.284	0.072	13.978	0.006	5.292	0.050
Rem	0.002	0.962	0.478	0.509	0.007	0.937	0.199	0.667
Fert $\times$ Rem	$< 10^{-3}$	0.991	0.514	0.494	4.356	0.070	0.033	0.861
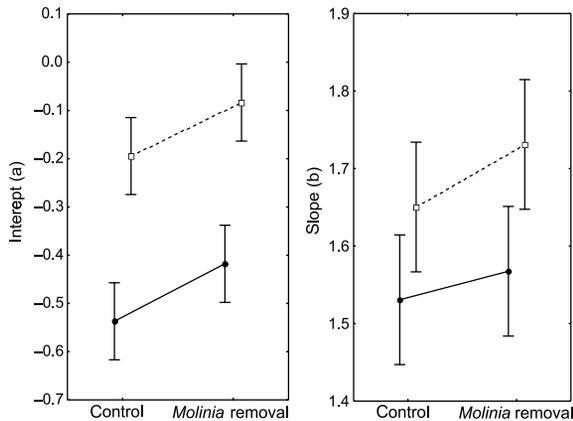
Fig. 4. Intercept and slope of Taylor's power law. The error bars denote 95% confidence intervals. Fertilized plots are shown by open symbols and broken lines, the non-fertilized by full symbols and full lines. Results of the two way ANOVA are in Table 3.

Fig. 5. Decrease of the coefficient of variation with mean species biomass. A non-fertilized control plot is used as an example. The line represents the fitted linear function: $cv = 0.6505 - 0.5167 \log(\text{mean})$. Decrease is highly significant ($P \ll 0.001$).

Downing (1994) and Tilman (1996) found lower stability in their fertilized treatments. Whereas Tilman and Downing (1994) ascribed their stabilizing effect to species diversity (the fertilized plots were less diverse and the effect of diversity was significant even after controlling for the fertilization effect in the multiple regression), we expect that this was mainly the effect of environmental productivity. This opinion is supported by the fact that the individual populations fluctuated more in the fertilized plots. This was true both for the variability described by Taylor's power law (where the difference was highly statistically significant in both parameters, intercept and slope), but also when individual species were compared across the treatments. Moreover, the effect on individual species was more pronounced than on the total biomass. This is in contradiction to predictions based on Lehman and Tilman's (2000) competition models. It seems that it was not the population structure of the community (characterized by the diversity), but nutrient availability that caused the differences in the variability. Plants that are not limited by nutrients can better "take advantage" of favorable weather conditions in a year. Once we alleviate nutrient limitation as a stress, other stresses such as water limitation become relatively more important. Since water availability shows greater interannual

variation than nutrient availability, the fertilized plots, which are likely to be primarily moisture limited, show greater variability in biomass production. This is consistent with Huston's (1997) interpretation of Tilman's (1996) results. In our previous studies (Lepš et al. 1982, Lepš 1990), the more productive community was also more variable. However, the communities differed in the constituent species strategy and we stressed the effect of species strategy (MacGillivray et al. 1995). The present results demonstrate that even the same species fluctuate more in the more productive environment.

The portfolio effect is affected mainly by two factors: how the variance is scaled with the mean, and whether the variability of individual species is correlated (Doak et al. 1998, Tilman et al. 1998, Cottingham et al. 2001).

Table 3. Two way ANOVA of the Taylor power law intercept and slope values in individual quadrats. The main effects are fertilization (Fert) and *Molinia* removal (Rem). For both main effects and interaction ($\times$), df effect = 1, df error = 8.

	Intercept		Slope	
	F	p-level	F	p-level
Fert	95.455	$< 10^{-3}$	15.233	0.005
Rem	11.047	0.010	2.623	0.144
Fert $\times$ Rem	0.014	0.908	0.369	0.561
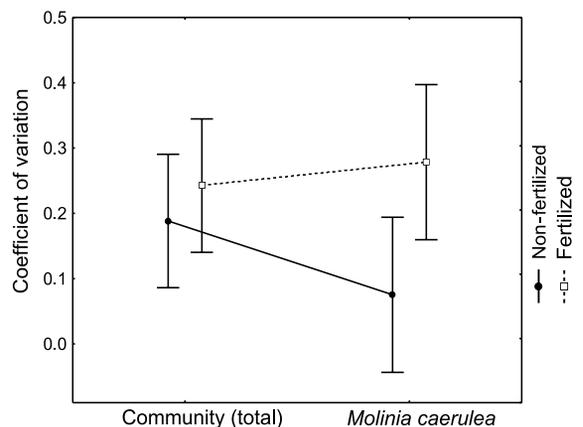
Fig. 6. Variability of total community biomass and of *Molinia caerulea*. In the split-plot ANOVA, only the Fertilization $\times$ Removal interaction was significant ($P = 0.046$).

The strongest effect is expected when the CV remains constant, which corresponds to a slope of 2 in Taylor's power law (we do not consider the unlikely situation of CV increasing with mean biomass.) We found the slope in Taylor's power law being between 1.5 and 1.7, which corresponds with the value of the CV decreasing with the average. When the species fluctuate independently of each other, the portfolio effect disappears when the slope equals 1. (If their fluctuations are positively correlated, then even at higher values.) The cases where the slope is below 1 are very rare, if any. Consequently, the predictions of Hughes and Roughgarden (2000) which are based on the assumption that variances are independent of mean abundances (which is equivalent to the slope being zero), have to be taken with extreme caution.

In 10 of the 12 plots, the sum of species variances was higher than the variance of total biomass. This shows a positive correlation among species and also suggests a weakening of the portfolio effect and the highly unequal dominance-diversity pattern further diminishes its importance (Schwartz et al. 2000). The positive correlation further suggests that the concordant response of the species to environmental variation was stronger than the possible effect of species complementarity (i.e. of a species taking advantage of a weakened competitor in a community). In our case, the species were probably similarly influenced by water availability. The two cases with discordant species response were probably caused by species demography. At a plot size 0.25 m², a single individual of the flowering monocarpic *Cirsium palustre* might form a large part of the biomass. The energy for flowering had been stored underground during the previous year(s). In the two plots, flowering *Cirsium* appeared just during the second year, i.e. the year with the lowest biomass. However, the fact that some species were able to "store" the energy gained during a favorable year underground and increase their productivity in the subsequent year (whereas others increase their productivity immediately) is undoubtedly a mechanism by which diversity can stabilize aboveground productivity.

The insurance effect (Yachi and Loreau 1999, Loreau 2000, Ives et al. 2000) is very similar to the portfolio effect. Whereas the independence of species variation (i.e. low or negative covariance) is stressed in the portfolio effect, Yachi and Loreau (1999) stress the difference among species' productivity response. However, the bigger is the difference in species response, the lower will be the covariance of the species. Whereas the description using the species' responses is more mechanistic, the covariance is easier to measure in the experiments. Both descriptions can be considered as mathematical expressions of the original idea of MacArthur (1955), when proposing the Shannon formula as a measure of stability. The aggregate community characteristics will be stable when a species failure can be compensated for by other species present in the community.

In the non-fertilized plots, the dominant species, *Molinia caerulea*, was more stable (as measured by CV) than the total community. Also, this shows that some species (and particularly dominants) might be more stable owing to their traits. *Molinia* stores nutrients in the basal internodia, which might buffer against environmental fluctuations. Also, rather long strong roots enable this species to reach the underground water. A similar mechanism (underground storage organ) is also present in another "stable species", *Potentilla erecta*. However, the whole problem needs further investigation.

The extremely stable *Molinia caerulea* suggests a model of community functioning, in which stable dominant(s) are complemented with sub-ordinate species, which are more variable in time. We can expect this model to work in communities with naturally developed dominance structure. It is even possible that the ability to buffer environmental fluctuations might help the species to attain its dominance. A case, where removal of a grass dominant *Lolium perenne* enhanced spatial variability of both the biomass and net primary productivity was reported by Wardle et al. (1999).

Whereas the increase of diversity by the removal of the dominant did not lead to decreased variability of community biomass, fertilization caused increased variability. It is likely that it was not diversity itself, but rather environmental productivity that was the main determinant of community variability. The dominant species was more stable than the whole community biomass, which suggests the importance of species strategies as determinant of species stability, as suggested by Lepš et al. (1982).

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