

Stability may decrease with diversity in grassland communities: empirical evidence from the 1986 Cantabrian Mountains (Spain) drought

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Frank and McNaughton reported that community stability, measured by the resistance to change in species composition when perturbed by drought, increased with species diversity in grasslands of Yellowstone, USA. They also found that species diversity increased with spatial heterogeneity of the community, pattern diversity. In a similar study of grasslands in the Cantabrian Mountains, we found exactly the opposite; when affected by drought, the resistance of these communities to change in species composition decreased as diversity increased, and diversity was not related to spatial heterogeneity. The contrasted results in Yellowstone and Cantabrian grasslands match theoretical predictions derived from model systems and suggest the existence of complex relationships between diversity and community stability.

Material and methods

The effects of a severe regional drought on plant species composition were studied in 20 sites in the Reyero Valley, Cantabrian Mountains, north-west Spain. The data are part of a study on the influence of cattle grazing on the structure of grassland communities (Rodríguez 1992). The area is geologically diverse, varying from massive limestone and calcareous conglomerates to sandstone or quartzite. The valley floors and lower slopes are of alluvial and colluvial materials. The altitude varies from 1000 to 1900 m, although the grasslands studied were all between 1150 and 1400 m. The climate is transitional between Mediterranean-continental and Atlantic, with a mean annual precipitation of 1220 mm. The mean minimum and maximum temperatures range from -3 to 29°C with extremes of -11 and 32°C, respectively. Only three months are guaranteed frost-free (typically from June to August), while for five months frosts are normal (from November to March), the remaining months have occasional frosts.

The vegetation has characteristics associated with both types of climate, and varies according to altitude and exposure. Plant growth stops during the coldest winter months, and from late July to early September due to summer drought (e.g. Rivas-Martínez et al. 1984). The grasslands studied were dominated by herbaceous perennial forbs and grasses with few annual species. Some shrub species were invading the grasslands, but never exceeded 20% of the species. A detailed description of these communities is given in Rodríguez, Borges and Gómez-Sal (unpubl.). Briefly, these communities are of four types: mesic grasslands on acidic parent materials with low grazing pressure (1); xeric grasslands on calcareous parent materials intensively grazed in early spring

Does diversity tell us anything about the stability of the ecosystems? Early theoretical work, logically simplistic (see Pimm 1984), argued that increased complexity enhanced ecosystem stability (e.g. Elton 1958). More sophisticated theoretical studies concluded just the opposite, i.e. that more complex ecosystems are less likely to be stable than simple ones (e.g. Gardner and Ashby 1970, May 1972), or suggested complex relationships between community stability and diversity (King and Pimm 1983, Pimm 1984; see also Margalef 1980). The question of how diversity and stability are related in natural ecosystems remains unanswered, mainly because empirical studies are still uncommon (Pimm 1984, Kikkawa 1986; but see McNaughton 1977, and Witkowski 1978). Recently, Frank and McNaughton (1991) found that resistance to drought-induced species composition change and species diversity (H') were positively correlated in grasslands of Yellowstone National Park. Here, we show that the contrary may occur in similar types of communities.

Table 1. Species diversity (H'), species richness (S), number of species showing significant shifts in relative abundance ($\#\Delta$), evenness (J') and resistance (R) in 19 grasslands. Community type codes are as in Fig. 1. Community types have been arranged in increasing order of grazing pressure (i.e. $1 < 2 < 3 = 3'$).

Grassland	Community type	H'	S	$\#\Delta$	J'	R
2	1	1.33	26	1	0.408	0.988
4	1	1.23	21	2	0.406	0.908
8	1	1.32	28	2	0.396	0.910
13	1	1.38	28	3	0.414	0.852
17	1	1.16	28	7	0.348	0.843
19	1	1.16	19	1	0.394	0.972
32	1	0.98	14	1	0.370	0.999
42	1	1.34	32	4	0.388	0.858
47	1	1.04	25	0	0.322	1
11	2	1.32	32	3	0.381	0.755
33	2	1.18	21	3	0.386	0.947
36	2	1.16	16	2	0.420	0.996
1	3	1.22	28	3	0.367	0.789
5	3'	1.47	31	6	0.427	0.863
7	3	0.92	18	1	0.318	0.987
15	3	1.32	23	5	0.422	0.742
16	3'	1.58	28	6	0.473	0.809
38	3	1.35	27	1	0.409	0.856
40	3	1.11	14	2	0.420	0.830

(2); and mesic grasslands on acidic (3) and calcareous (3') parent materials intensively grazed through spring. The categories of grazing regime were established from direct observations and information provided by farmers. All the grasslands were grazed by cattle, mainly dairy cows. The populations of wild herbivores, such as chamois (*Rupicapra rupicapra*) and roe deer (*Capreolus capreolus*), are not important in these grasslands because they normally occur at higher elevations. We did not detect overgrazing effects in any of the intensively grazed grasslands.

The study spanned 1986 and 1987. The total precipitation between 1 January and 31 May for these years was 72% and 76% of normal, respectively. January–March precipitation was 288 mm for 1986, and 302 mm for 1987; whereas April–May precipitation was 115 mm for 1986, and 125 mm for 1987. The greatest differences between the years occurred in June–July, when the precipitation was only 20 mm in 1986, but was 129 mm in 1987, equalling 19% vs 123% of the average precipitation, respectively. The sites, each 10 m × 10 m, were sampled in late July in both years, coinciding with the end of the growing season and after grazing was finished. For the estimation of the species biomass, four randomly-positioned 20 cm × 20 cm and 15 cm deep soil blocks together with the above-ground vegetation were removed from each site. The plant material was sorted into species, divided into above- and below-ground portions, dried in a drying oven at 60°C for 48 h, and weighed. The analyses involving below-ground biomass will be presented elsewhere. One site was omitted from the analyses as it was

close to a stream from which it received abundant water supply. This site did not show any change in relative species abundance.

Diversity was calculated as the Shannon-Wiener index (Shannon and Weaver 1949), i.e.

$$H' = - \sum_{i=1}^n p_i \ln p_i$$

where p_i is the proportion of the i th species' biomass in the community n , and evenness as $J' = H'/H'_{\max}$ (Pielou 1975). Resistance (R) of species composition to change was measured by means of the index used by Frank and McNaughton (1991), i.e.

$$R_j = 1 - \sum_{i=1}^n (\Delta p_{ij}/2)$$

where p_{ij} is relative abundance of the i th of the n species in community j exhibiting significant ($P < 0.05$) differences (Δ) between 1986 and 1987. The data analyses involved Pearson correlations, multiple regression analyses with backwards elimination and analyses of variance (ANOVA). Proportional data were angularly transformed, absolute data, except H' , were subjected to logarithmic transformation, whereas data of species counts were subjected to square root transformation [$X' = (X + 0.5)^{1/2}$] before analysis.

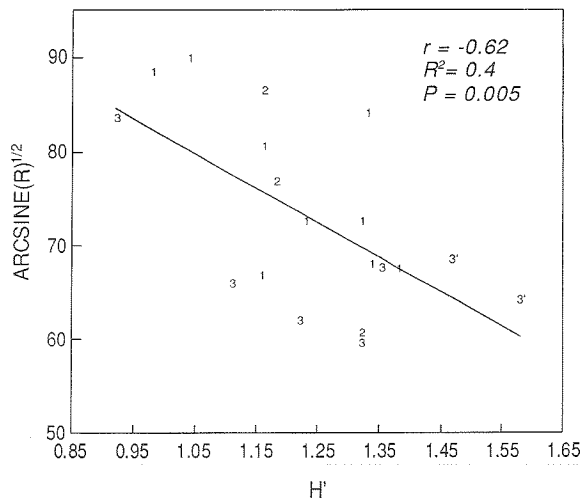


Fig. 1. Negative relationship between angularly transformed resistance (R , in degrees) and diversity (H'). Codes are mesic grasslands on acidic parent materials with low grazing pressure (1), xeric grasslands on calcareous parent materials, intensively grazed in early spring (2); and mesic grasslands on acidic (3) and calcareous (3') parent materials, intensively grazed through spring.

Results and discussion

Species diversity (H'), resistance (R), numbers of species exhibiting significant change ($\#\Delta$), species richness (S) and evenness (J') at the study sites are shown in Table 1. H' was positively related to its two components, i.e. S and J' ($r=0.7$, $P<0.001$ and $r=0.77$, $P<0.001$, respectively). Contrary to the Yellowstone case, R was negatively related to H' (Fig. 1). This was mainly due to the negative relationship between R and S ($r=-0.54$, $P=0.018$), since R was only marginally related to J' ($r=-0.42$, $P=0.07$). The number of species exhibiting significant change ($\#\Delta$) was positively related to H' and S ($r=0.59$, $P=0.008$ and $r=0.46$, $P=0.04$, respectively). This contributed to the inverse relationships of R with H' and S , since $\#\Delta$ and R were negatively related as well ($r=-0.7$, $P<0.001$). This result contrasted with the Yellowstone case too, as among these grasslands there was no relationship between $\#\Delta$ and R (see Frank and McNaughton 1991).

A positive relationship between resistance and diversity found in the Yellowstone grasslands was also found when grazed and ungrazed grasslands were analysed separately (Frank and McNaughton 1991). According to these authors, "the similar responses to drought of grazed and ungrazed vegetation indicates a dominant role of weather in the response measured in both the presence and absence of large herbivores". Similarly, in our case, resistance of intensively grazed grasslands and non-intensively grazed grasslands were negatively correlated with H' when analysed independently ($r=-0.6$, $P<0.07$ and $r=-0.7$, $P<0.05$, respectively). In spite of this, as the grasslands studied here were all grazed, still remains the question of whether grazing conditioned the relationship showed by resistance and diversity, in particular, since grazing intensity was also marginally negatively related with R ($r=-0.44$, $P=0.06$). Grazing was not related to either H' or any other parameter or environmental factor ($P\geq 0.25$ in all the cases). To remove the effects of grazing from the data, we repeated all the preceding analyses over the residuals (hereafter called R_r) resulting from the regression of R on grazing pressure. The results did not vary; i.e. R_r was significantly negatively related with H' , S and $\#\Delta$ ($-0.66 < r < -0.6$, $P\leq 0.007$ in all cases), whereas it did not show significant relationship with J' ($r=-0.33$, $P=0.16$).

In addition to these results, the data also indicate an important role of drought in determining the changes of species composition that occurred in the grasslands. Thus, there was a positive significant relationship between elevation and R_r ($r=0.5$, $P<0.03$), while elevation was not related to either H' , S , or J' ($P\geq 0.1$ in all cases). Since potential water stress diminishes as altitude increases, this meant that community resistance to drought was related to water availability. No other variable measured, slope, soil pH, percentage of nitrogen and organic matter, available phosphorus, and potassium, was related with R_r (detailed description of the environmental char-

acteristics of the sites will be provided elsewhere: Rodríguez, Borges and Gómez-Sal unpubl.). In spite of these results, species diversity was more important than elevation or any other variable measured in determining the resistance of the communities, since H' was the only variable loaded in a multiple regression analysis to describe R_r (note that to avoid multicollinearity among independent variables, S , J' and $\#\Delta$ were not included in this analysis as they were all significantly related to H' ; see Zar 1984). Moreover, a partial correlation analysis that controlled for the potential confounding effects of altitude showed a significant dependence of R_r on H' ($r_{\text{partial}}=-0.5$, $0.01 < P < 0.05$), which was greater than the dependence of R_r on altitude when H' effects were eliminated ($r_{\text{partial}}=0.4$, $0.05 < P < 0.1$). Therefore, the correlation of species diversity with resistance did not arise through altitude effects. (Analyses using R instead of R_r yielded similar results).

It is not possible to explain the differences between the Cantabrian and Yellowstone grasslands with the available data. Nevertheless, some suggestions are possible based on the parameters obtained in both areas and previous work. In Yellowstone, H' increased as a result of microsite dissimilarity of species composition and not as a result of an increase in microsite richness (see Frank and McNaughton 1991). We have also explored this aspect, although the scale of our analyses was necessarily different, since we used a direct method to estimate species biomass, whereas in Yellowstone this was done with the canopy intercept method. Thus, instead of calculating microsite richness as the average number of species contacted per pin, as in Yellowstone, we estimated the average number of species per quadrat of 20 cm \times 20 cm, our elemental sampling unit. This meant that the concept of microsite in our study refers to a wider area than in Yellowstone. In addition, we have also estimated the pattern diversity, i.e. the amount of within-community dissimilarity in species composition (Frank and McNaughton 1991; see also Pielou 1974), and looked at the relationships of this and the former parameter with H' . We found a marginally significant correlation between pattern diversity and H' ($r=0.4$, $P=0.063$), which contrasts with the strong positive relationship showed by these parameters in Yellowstone. Furthermore, the average number of species per quadrat was highly correlated with H' in our case ($r=0.71$, $P<0.001$), whereas there was no such relationship in Yellowstone. In sum, in the Cantabrian grasslands, species diversity increased mainly as a result of an increase in microsite richness, whereas microsite dissimilarity of species composition had only a marginal effect upon diversity.

In spite of the differences in scale, the clearly contrasting results obtained suggest that in the Cantabrian grasslands there was no stabilizing effect of microsite heterogeneity that seemed to exist in Yellowstone. This was the reason adduced by Frank and McNaughton (1991) to explain the increase of community resistance with species richness. In fact, a similar suggestion emerged from

the results obtained in model systems (Gardner and Ashby 1970, May 1972; see also Allen et al. 1993). Those models predict an increase in ecosystem instability as species richness increases, as has been found in the Cantabrian communities. The models also predict that the probability of being stable is higher in communities in which species interactions are organized into separate blocks of "micro-communities" (see May 1972). Accordingly, the positive relationship between microsite heterogeneity and diversity found in Yellowstone could explain the increased community stability observed in this place as species richness increases.

A point that may be of particular interest to modellers, although we do not have enough information to interpret it, is that the Cantabrian grasslands showed significantly lower evenness than the Yellowstone grasslands ($F_{1,34} = 174.12$, $P \ll 0.001$). Consequently, species diversity was lower in the Cantabrian communities than in those from Yellowstone ($F_{1,34} = 59.2$, $P \ll 0.001$), since there were no differences in species richness between the two areas ($F_{1,34} = 1.2$, $P = 0.3$). This result is suggestive; it implies that the relationship between stability and species diversity may vary depending on the degree of equitability of the species abundances (cf. King and Pimm 1983). In other words, it suggests that among communities with relatively low evenness (as in the Cantabrian grasslands), resistance to disturbance-induced species composition change tends to decrease as species richness increases, whereas when the evenness is higher (as in Yellowstone) the opposite occurs.

Finally, there is a strong possibility that different grazing histories in the Cantabrian and Yellowstone grasslands were related to the contrasting results obtained in each area. The grasslands studied in Yellowstone were grazed by native ungulates, mainly by bison (*Bison bison*) and elk (*Cervus elaphus*), which probably have been grazing there in large numbers over the centuries (see Frank and McNaughton 1992). In contrast, the Cantabrian Mountains have been man-managed for a long time (Martín-Galindo 1987), probably even from the second century B.C., when Roman historians reported the existence of livestock raising practises in the mountains of the interior of Spain (Caro Baroja 1975). This suggests that the vegetation in Yellowstone and in the Cantabrian Mountains has evolved under very different grazing conditions, which may be associated with its different responses to drought.

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