

F. García Novo, F. Díaz Pineda y A. Gómez Sal, coords.

DIVERSIDAD BIOLÓGICA Y BIODIVERSIDAD



FUNDACIÓN RAMÓN ARECES
MADRID, 2006

Biodiversity and stability in grassland communities

M. A. Rodríguez¹, B. A. Hawkins² & A. Gómez-Sal¹

¹Área de Ecología, Universidad de Alcalá, Alcalá de Henares (Madrid), España

²Department of Ecology and Evolutionary Biology, University of California, Irvine, USA

Introduction

In a paper by Tilman and Downing published in *Nature* in 1994 the authors concluded that their data support the diversity-stability hypothesis. Contrary to this conclusion, we argue that Tilman and Downing's data actually support an alternative hypothesis: the species redundancy hypothesis. In the present work, we also tested these hypotheses using data on grassland diversity. We examined the effects of a regional drought on plant community biomass in 19 native grasslands in the Cantabrian Mountains, Spain. Our study spanned 1986 (a dry year) and 1987 (wet). We found (like Tilman and Downing for communities of >10 species) that the rate of change in biomass is independent of species richness in grasslands ranging from 14-32 species. We also found that the rate of change in biomass was associated with plant evenness (J'), in that communities with high evenness changed little between the years, whereas plots with low evenness showed larger differences. As a result of this relationship, the change in biomass was also associated with species diversity (Shannon's H'). These data support an alternative view of the importance of species diversity that argues that it is the evenness of the community, rather than species richness per se, that confers stability.

Attention to the role of diversity in the stability of natural ecosystems has increased in recent years with the publication of several field and experimental studies. Among them, a paper by Tilman and Downing which was published in 1994 has played a key role (3). These authors

concluded that their data support the diversity-stability hypothesis, but not the species redundancy hypothesis. This conclusion was based on a positive, curvilinear relationship between species richness (Tilman and Downing's measure of diversity) and community resistance to drought. However, as Tilman and Downing pointed out, their results did not allow them to 'reject the hypothesis that the relationship [between species richness and community resistance to drought] may reach a plateau', since such relationship was no longer significant in grasslands of about 10 or more species. Indeed, the species redundancy hypothesis states that, because most species are functionally redundant, ecosystem function is independent of species richness so long as major functional groups are present. So, what Tilman and Downing's data actually suggest is that this requirement may be met in grasslands of about 10 or more species. In the present work, we also test the diversity-stability and redundancy hypotheses using data on grassland diversity.

Methods

The effects of a severe regional drought on plant species composition were studied in 20 sites in the Rezero Valley, Cantabrian Mountains, North-West Spain. The area is geologically diverse, varying from massive limestone and calcareous conglomerates to sandstone or quartzite. The climate is transitional between Mediterranean-continental and Atlantic, with a mean annual precipitation of 1220 mm.

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 summer drought. The grasslands studied were dominated by herbaceous perennial forbs and grasses with few annual species. Some shrub species were invading the grasslands, but never exceed 20% of species. A detailed description of these communities is given elsewhere (1, 2).

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 both 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 x 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 x 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 change in relative species abundance.

Diversity was calculated as the Shannon information index (H'), and evenness (J') as $H'/\ln S$, where S is species richness. Rate of change in biomass (R) was measured as $\ln(\text{biomass}_{1986}/\text{biomass}_{1987})$, where biomass_{1986} was at the height of the drought, and biomass_{1987} was for the year following the drought. A value of 0 represents no change in biomass between years, and high negative values represent large decreases. The data were investigated with multiple regression analyses.

Results and Discussion

We found (like Tilman and Downing for communities of >10 species) that the rate of change in biomass is independent of species richness in grasslands ranging from 14-32 species ($R = -0.998 + 0.016S$, $r^2 = 0.044$, $P = 0.391$) (Fig. 1). However, we also found that the rate of change in biomass was associated with plant evenness (J'), in that communities with high evenness changed little between the years, whereas plots with low evenness showed larger differences ($R = -3.057 + 6.223J'$, $r^2 = 0.268$, $P = 0.023$). As a result of this relationship, the change in biomass was also associated with species diversity ($R = -2.310 + 1.370H'$, $r^2 = 0.253$, $P = 0.027$).

These data support an alternative view of the importance of species diversity that argues that it is the evenness of the community, rather than species richness per se, that confers stability. This 'evenness-stability' hypothesis predicts a clear

alternative pattern to the hypothesis tested by Tilman and Downing. It predicts that community stability is independent of its species richness but is positively associated with the relative abundances of its constituent species.

In conclusion, we suggest that hypothesized relationships between species diversity and community stability and function that depend solely on the richness component of diversity may miss a critical aspect of biodiversity, and that more detailed information on system structure may be necessary for assessing the impact of species removal on community function.

References

- (1) Rodríguez, M. A., Borges, P. A. V. & Gómez-Sal, A., 1997. Species and life-forms composition of Mediterranean mountain pastures in two years of contrasting precipitation. *Flora*, 987: 1-10.
- (2) Rodríguez, M. A. & Gómez-Sal, A., 1994. Stability may decrease with diversity in grassland communities: empirical evidence from the 1986 Cantabrian Mountains (Spain) drought. *Oikos*, 71: 177-180.
- (3) Tilman, D. & Downing, J. A., 1994. Biodiversity and stability in grasslands. *Nature*, 367: 363-365.

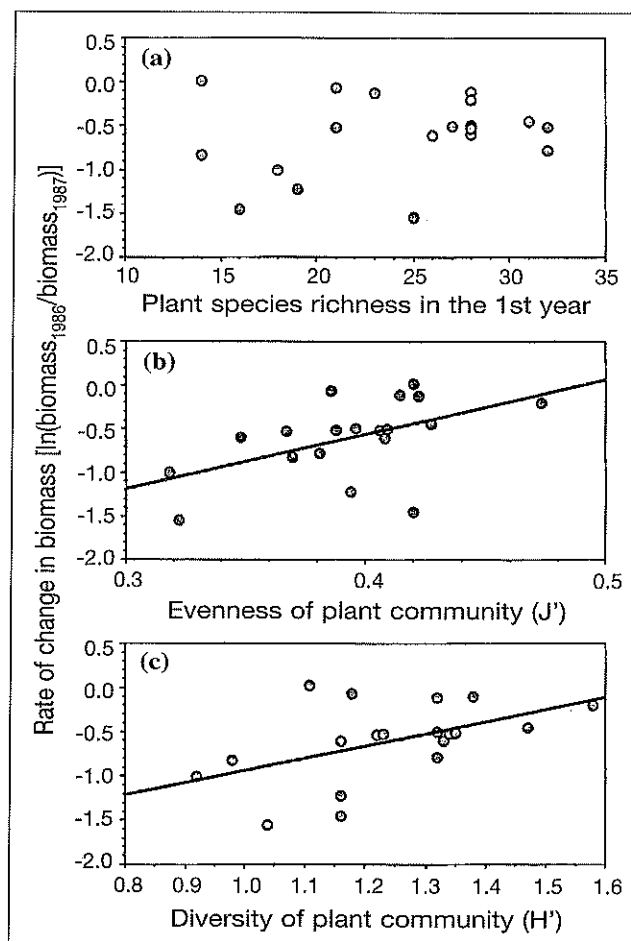


Fig. 1. Relationships between the relative rate of change in plant community biomass and (a) plant species richness, (b) plant evenness, and (c) plant diversity, in 1986.

Reservados todos los derechos.

Ni la totalidad ni parte de este libro puede reproducirse o transmitirse por ningún procedimiento electrónico o mecánico, incluyendo fotocopia, grabación magnética, o cualquier almacenamiento de información y sistema de recuperación, sin permiso escrito de Editorial Centro de Estudios Ramón Areces, S. A.

Imagen de portada: Delta del río Lena en el Mar Ártico de Laptev, Siberia. El delta, de unos 45,000 Km², forma parte de la Reserva de vida silvestre Delta de Lena, de 61,000 Km². Imagen en falso color combinando bandas del Landsat 7, tomadas el 27-7-2000. Cedida por USGS Natural Center for EROS and NASA, Landsat Project Science Office.

© F. García Novo
F. Díaz Pineda
A. Gómez Sal

© EDITORIAL CENTRO DE ESTUDIOS RAMÓN ARECES, S.A.
Tomás Bretón, 21 - 28045 Madrid

© FUNDACIÓN RAMÓN ARECES
Vitruvio, 5 - 28006 Madrid

Depósito legal: M-45759-2006

Impreso por ANEBRI, S.A.
Antonio González Porras, 35-37
28019 Madrid

Impreso en España / *Printed in Spain*